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NESTING AND PRODUCTION OF THE RING-NECKED
PHEASANT IN NORTH-CENTRAL IOWA

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NESTING AND PRODUCTION OF THE RING-NECKED PHEASANT IN NORTH-CENTRAL IOWA

INTRODUCTION

From the time of its inception in the autumn of 1935, until 1942, the program of the Iowa Cooperative Wildlife Research Unit included life history and management studies of the ring-necked pheasant (*Phasianus colchicus torquatus* Gmelin) on the Winnebago Experimental Area in north-central Iowa. During the first three years emphasis was placed on the food and cover relationships in winter survival (Green and Beed, 1936; Green, 1938 and unpublished reports). Beginning in 1939, special attention was directed to the reproductive phase of the pheasants' life cycle.

This paper treats data gathered on the Winnebago Area from April until September in the years 1939, 1940, and 1941. Some of the data collected in 1939 have already appeared in published form (Baskett 1941).

The pheasant, exotic in Iowa, now occurs in shootable numbers over a large part of the northern half of the state. In general, it is most numerous within Iowa on the intensively farmed land of the Iowa and Wisconsin drift areas and the northern parts of the Missouri and Mississippi loess areas.

The fact that the pheasant has established itself, maintained its numbers, and increased, is indicative of its adjustment not only with climatic and other general environmental factors as they exist in northern Iowa but also with the intensive type of agriculture here practiced.

This investigation pursued the following objectives: (1) to extend the knowledge of pheasant behavior, (2) to examine the nesting cycle of the pheasant in north-central Iowa, and (3) to determine, as far as possible, the relationships between natural pheasant production and agricultural practices, weather, and other environmental conditions in north-central Iowa.

The research reported here was carried on under the administrative supervision of Dr. Carl J. Drake, Department of Zoology and Entomology, Iowa State College, Ames, Iowa, Dr. Thomas G. Scott, Leader of the Iowa Cooperative Wildlife Research Unit, Ames, Iowa, and Mr. Fred Schwob, then director of the Iowa State Conservation Commission, Des Moines, Iowa. Dr. G. O. Hendrickson, Department of Zoology and Entomology, Iowa State College, and Dr. Thomas G. Scott directed the research. Dr. Paul L. Errington, Department of Zoology and Entomology, Iowa State College, made helpful suggestions. To these men I am greatly indebted.

Mrs. Margaret M. Nee, Chicago, Illinois, contributed valued suggestions relative to pheasant behavior and territoriality. Dr. Paul D. Dalke, Leader of the Missouri Cooperative Wildlife Research Unit,

Columbia, Missouri, kindly gave advice on these same matters. Thanks are due the farmers on whose land the investigation was carried out. Especial appreciation is expressed to Messrs. O. B. Christenson, Tilford Christenson, C. O. Christenson, Clarence Johnson, C. L. Pierce, and Elmer Seim for their kindness in showing me nests they had found, and for help in various other ways. Acknowledgment is also due Maurice Provost, Ray Erickson, and Stirling Kyd for valued assistance.

The aid and encouragement given by Drs. Errington and Scott and Mr. Provost in the preparation of this paper have far exceeded the bounds of professional courtesy.

DESCRIPTION OF AREA

The Winnebago Research Area lies in sections 9-12, 13-16, and 21-24, Eden Township, Winnebago County, in north-central Iowa. (See Figures 1, 2, and 3.) Pheasant nesting and production research was performed on a plot of 1,520 acres, continuous, but irregular in shape and lying in only five of these sections (numbers 13, 14, 15, 23, and 24).

Winnebago County occurs entirely within the Wisconsin drift soil area, which is characterized by a generally flat or depressed topography, with few natural drainage channels, but with frequent lakes, ponds, and sloughs (Brown 1936; p. 9). The topography of the western part of the county is almost level to gently rolling, with low and rounded hills and ridges (Stevenson *et al* 1922; p. 8), and it was in this portion that the nest-research area was located. Except for two steep and relatively high ridges, the terrain was flat or moderately sloped.

In its primitive condition, vegetation of the nest research area consisted of plants of the high and low northern prairie, and of the marshes. With the advent of agriculture, the subsequent construction of drainage ditches, and the laying of tiles, the vegetation was greatly altered. A few sloughs present on the nest-study area retain much of their original vegetation, but no undisturbed prairies remain. Prairie plants are still found in native hayfields, fence rows, and road ditches, more or less interspersed with exotic species.

The land of the 1,520-acre area is intensively farmed. During the three years of research, an average of 1303.6 acres (92.4 per cent of the land) was put to direct agricultural use as hay, pasture, or crop land. Table 1 summarizes land-use on the nest-research area of 1940, and compares it with land-use of all Winnebago County farm land in 1940. The similarities are obvious. Detailed listing of crops and acreages for the 1,520 acres studied

TABLE 1. Comparison of Land Use for Winnebago Research Area and Winnebago County, 1940.

Crop	Winnebago Research Area 1520.0 acres		Winnebago County* 251,894 acres in farm land	
	Acres	Percentage of total	Acres	Percentage of total
Corn.....	426.10	28.0	70,611	28.1
Small grains, flax, sweet clover for seed, etc.....	478.40	31.5	66,160	26.3
Hay.....	206.20	13.5	32,633	13.0
Other crops (soybeans, beets, etc.).....	65.00	4.3	2,160	0.9
Pastures.....	208.10	13.7	54,087	21.5
All other waste, idle, farm groves, highways, etc.....	136.20	9.0	25,743	10.2

*Figures taken or calculated from Iowa Yearbook of Agriculture for 1940.

appear in Tables 2, 3 and 4, and the maps (Figures 1, 2 and 3) show field arrangement, and if examined successively, demonstrate the general trends in rotation. The basic scheme of rotation before the Agricultural Adjustment Act (AAA) was effective had been annual alternations of corn and oats in the larger fields, with irregular shifts to pasture and hay in the smaller tillable fields and in depleted portions of the larger ones. Meadows were used year after

year as sources of wild hay. Compliance with the AAA program resulted in increased acreages in hay land, idle land, small grain, and pastures, and led to many changes in sizes and shapes of fields. The latter conditions obtained throughout the period of study reported here.

During the years 1939, 1940, and 1941, the annual mean temperatures at Forest City, Iowa, about 20 miles southeast of the Winnebago Area, were 48.2, 45.7, and 48.7 degrees Fahrenheit, respectively. The total precipitation figures for these years were 24.23, 31.13, and 42.45 inches. (Reed 1939, 1940, and 1941.) Specific weather conditions in relation to agricultural activities and pheasant nesting are discussed later.

Several species of birds and mammals which were regarded as possible predators upon young or adult pheasants or the eggs were resident on or hunted over the nest-research area during the nesting seasons. Avian species included marsh hawks (*Circus hudsonius*), short-eared owls (*Asio flammeus flammeus*), red-headed woodpeckers (*Melanerpes erythrocephalus*), blue jays (*Cyanocitta cristata cristata*), eastern crows (*Corvus brachyrhynchos brachyrhynchos*), migrant shrikes (*Lanius ludovicianus migrans*), European starlings (*Sturnus vulgaris*), and

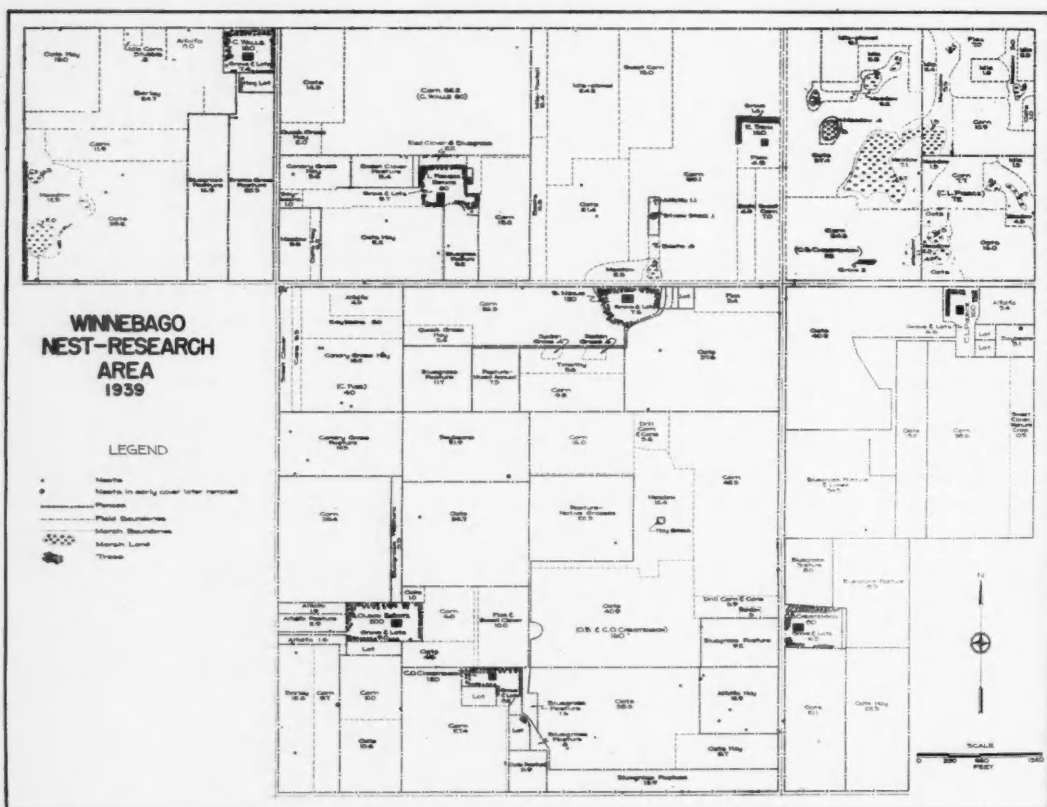


FIGURE 1

several species of blackbirds. The mammals included ground squirrels (*Citellus franklini* and *C. tridecemlineatus*), fox squirrels (*Sciurus niger rufiventer*), several species of mice, weasels (*Mustela* spp.), minks (*Mustela vison*), skunks (*Mephitis mephitis* and *Spilogale interrupta*), common badgers (*Taxidea taxus taxus*), and domestic cats and dogs. "Signs" of red foxes (*Vulpes regalis*) were seen on the nest-research area, but never with certainty during the nesting season.

TECHNIQUES OF INVESTIGATION

General observations of pheasant behavior were carried on early each spring by watching the birds closely from a parked car. Their movements were recorded on sketch-maps in the field notebook, accompanied by written descriptions of behavior. In 1941, an attempt was made to plot several of the "erowing areas" of males on a large scale map.

With the beginning of nesting each year, a system of patrolling the fields was inaugurated. Fields were gone over in rotational series until mowing was begun, but during hay mowing and harvesting, the cutting machinery was followed whenever possible, in an effort to obtain data on destruction of nests and injury to female pheasants. During these

periods, the rotational scheme was upset. Fields of small grain were not examined for nests until harvest, both because patrolling them periodically would have resulted in inadequate coverage of others, and because some damage to plants was feared.

When nests were found, their locations were paced off and later plotted on maps (Figures 1, 2, and 3), which were also used to record mowing and harvest dates, and to compute acreages. Nests were visited periodically, and notes were kept on dates, numbers, possible causes of disappearance of eggs, and on various details of nest ecology, including plants present, roofing, etc.

In order to avoid confusion of promiscuously dropped single eggs with actual nesting attempts, the writer considered for nesting records only groups of at least two eggs. Nests of other ground nesting species were examined for cases of parasitism by pheasant hens.

During the three seasons, location data were obtained for 533 nests; of these 75 were established in 1939, 140 in 1940, and 318 in 1941. Farmers reported 58 of the nests, but all were seen by the observer before they were counted as records.

When possible, estimates of the dates upon which nests were established, hatched, or would have

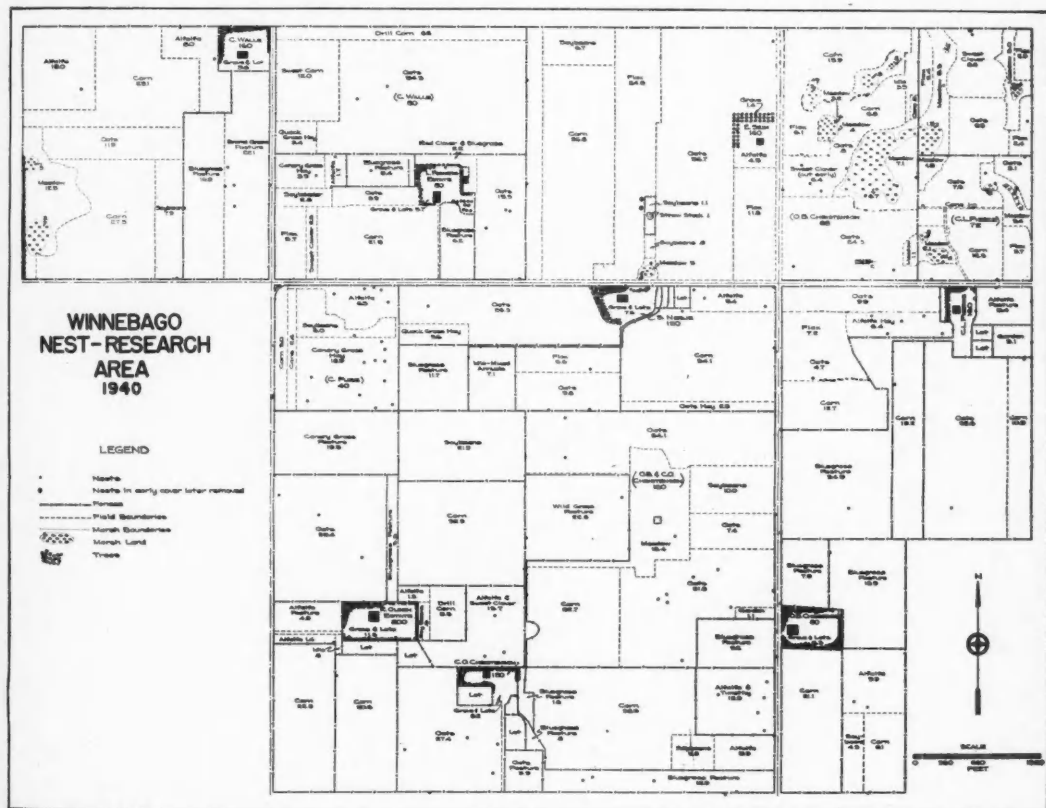


FIGURE 2

hatched were made by bi-monthly periods. These estimates were based on the following considerations as cases demanded: (1) general appearance of eggs in relation to weather conditions, (2) numbers of eggs, (3) approximate ages of embryos, and (4) appearance of hatched shells in relation to weather conditions.

Brood counts were made with facility from road-sides early in morning and late in evening. Estimates of the ages of wild chicks were based on observations of the growth of a few pen-raised young each year.

Enumeration data were derived in the spring from repeated observations on the nest-study area and by a modified spot-census method. Enumerations were accomplished in the fall by flushing counts during the hunting season and by roadside counts made according to the method of Bennett & Hendrickson (1938).

COURTSHIP, TERRITORIALITY, AND NESTING HABITS

WINTER AGGREGATIONS

In the winter, pheasants often congregate in dense cover. In Michigan, Wight (1930) found that marshes were their principal winter haunts. In the

sandhills region of Nebraska, Sharp and McClure (in McAtee *et al* 1945) found them wintering along marshes and streams that had willow thickets and adjacent meadows, in shelter belt areas, and in cattle lots which had woody cover nearby. On the Winnebago Area, the principal coverts used in winter were small potholes, willow thickets, and farm groves. The degree of concentration in these coverts was related to severity of weather (Green 1938).

In their winter groups, the pheasants are sometimes segregated by sex and sometimes not. "Male bands" are frequently seen, but they appear to be loosely knit and to vary in size from day to day. Loose flocks of females are also to be found, but a few males are generally present with large groups of hens. Wight (McAtee *et al* 1945) observed a general segregation of sexes in winter, but found groups containing both sexes where food was abundant or cover restricted.

SPRING DISPERSAL

In early spring, the males become progressively less companionable and by March immediate proximity of two usually results in strife. The females gradually disperse as small groups but probably

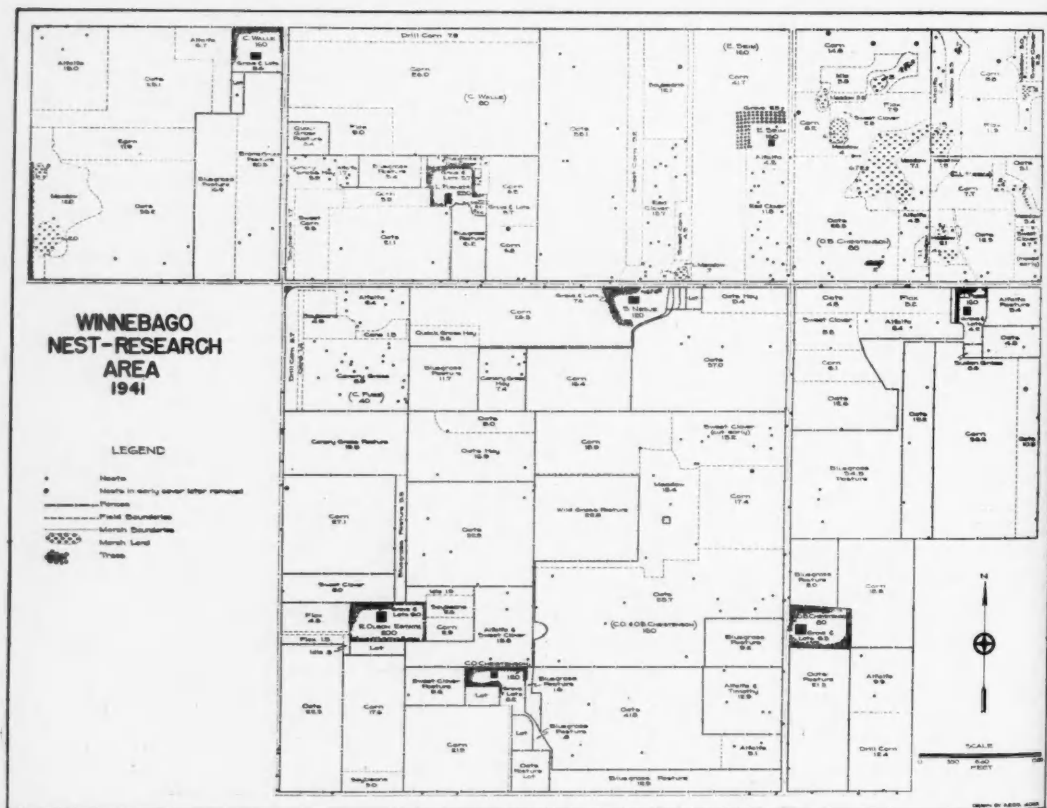


FIGURE 3

are solitary only while incubating; even then they may consort with other females and a male during rest periods. Concurrent with the breaking up of winter bands of pheasants, there is a movement away from winter coverts which finally results in a much more nearly uniform local distribution of the birds.

CROWING

As dispersal progresses, the males begin crowing. In crowing, the male grasps a relatively immovable object with the claws, stands very erect, and emits a dissyllabic sound "resembling the imperfect attempts of a young fowl" (Tegetmeier 1904, p. 12); then follows a rapid movement of the wings which produces a booming sound. Crowing was heard on the Winnebago Area at the earliest date (March 21, 1939) that the writer arrived there in the spring, and it was continued until late summer, although it was heard infrequently after the first of July. Crowing occurred most frequently on clear, still days during two diurnal periods. One of these periods immediately followed sunrise and the other preceded sunset, each of them lasting about two hours. Throughout these periods pheasants fed extensively, and engaged in activities relating to mating behavior. During intemperate weather, the times of all diurnal activities are often altered, and rules for crowing behavior to fit all weather conditions are difficult to formulate.

From March 21 until April 15, 1939, crowing was observed and recorded 102 times; 54 males were involved. In only four of the 102 observations did a male crow in the same place more than once. One male was seen crowing eight times consecutively, each time in a different location. The observations indicated no definite association of crowing with landmarks such as stones, but the males were often at some local point of vantage during the act. Of 102 crowing places, 18 were located at or near the top of a hill or ridge one foot or more in height; 18 were located on prominences less than one foot high (corn hills, tufts of sod, etc.); 59 were not on prominences; and the remaining seven were not classified in this respect. In the 59 observations in which the males were not on prominences, they were in bare fields, heavily grazed pastures, or other situations which permitted them to be relatively conspicuous by means of the very erect pose. Crowing was sometimes heard in heavy cover where the male was not seen by the writer; despite this fact, the males usually made themselves locally conspicuous while crowing.

In his discussion of crowing among pheasants, Leffingwell (1928) wrote that of three birds observed, one used a rail fence from which to challenge, but the others had no special perch. He added, however, that the crowing place is usually more trampled down than a roosting place, leaving the reader with the impression that specific crowing sites were used with considerable frequency. So far as I could determine there were few, if any, special spots for crowing, although some males exhibited preferences

for certain large hilltops or hillsides. Any locations which permitted the males to be locally conspicuous seemed satisfactory on occasion, and any returning to an exact spot used before for crowing seemed accidental.

THE DISPLAY

During the period when crowing is most frequent, female pheasants, either singly or in groups, slowly traverse the feeding grounds. They are frequently escorted by one male, then another, the individual males tending to remain each within an area. While escorting hens, a male feeds, crows, and often displays to females. The display consists of spreading and extending the wing downward on the side toward the female, and of spreading the tail and tilting its top in the direction of the hen; during this procedure the male's neck is somewhat bowed and the feathers of the neck are ruffled. Early in April, the female may watch the male briefly and then continue feeding or walk around him. The male then contrives to put himself in front of the hen and displays again. Sometimes the female runs from the male as if to escape his ardor. As the nesting season approaches, the hens become more attentive and may crouch by the displaying male as he holds his pose for several minutes. With the onset of nesting, the females are seen less in their wanderings.

COPULATION

Copulation is performed much as in the domestic fowl (*Gallus gallus*) apparently with or without being preceded by the display.

POLYGAMY

Wild pheasants are generally assumed to be polygamous and this investigation revealed no evidence to the contrary. Single males were often seen consorting with more than one female at a time, and despite the presence of at least twice as many females as males each year, there was no reason to suspect the presence of large numbers of unmated hens.

The events in the pheasant's life cycle from winter to the onset of nesting, including courtship, have been described at least in part by numerous authors, including Tegetmeier (1904); Townsend (1920); Leffingwell (1928); Pycraft (in Kirkman & Hutchinson, 1936); and Wight (in McAtee *et al* 1945), and except as noted, the outline of the events presented above is in general agreement with the findings of these authors.

TERRITORIES

LOCALIZATION OF COCKS IN SPRING AND SUMMER RANGE

In the Winnebago investigation, several males which were individually distinguishable were seen repeatedly in the same general localities throughout the spring. For example, a male which had a distinctive light colored nape and a high, squeaky voice was observed from March 31 until April 14, 1939, in an area of about 55 acres, consisting of the edge

of a farm grove, a plowed field, and a weedy pasture. He was found dead in the weedy pasture on April 20. In 1940, a male which limped slightly was seen often in either of two adjacent plowed fields, the fence row between them, or a road ditch bordering them. The conclusion drawn from several observations like these was that the localization of each male through April until mid-May (after which the author's attention was directed mainly to finding nests) and probably throughout the breeding season, was a phenomenon of general occurrence. Limited banding experiments indicated that at least some males were to be found in the same localities in October, a finding in agreement with Wight's (McAtee *et al* 1945).

TERRITORIES OR "CROWING AREAS"

Leffingwell (1928) regarded the pheasant as a territorial species. He wrote that the purpose of crowing seems to be to announce that a certain area has been claimed by a male who is ready to fight for its defense, and that the instinct to protect the chosen territory is developed about the time when the birds begin to display, but is at its maximum during the nesting season.

Wight (McAtee *et al* 1945) described the spring and summer pheasant range as broken up into many small units, each in the possession of an individual cock which zealously protects it by driving off all other males. The units were termed "crowing areas" because they are distinguished by the call of the cock, and the term "crowing area" was held to be synonymous with "territory" in the technical sense. In the same publication, Wight wrote that the extent and shape of the crowing areas are determined by the composition, density, and arrangement of the cover, and that a patch of brush or woods is an essential part, although during the last of June hayfields provide sufficient shelter. Wight apparently regarded the "crowing areas" as very definitely delineated units, for he wrote (1939) that they were mapped for a period of five years in various places and that management plans were developed from information derived from the maps. Agreement with the concept of definite crowing areas is at least implied in the writings of many observers (Gould 1939 in New Hampshire; Randall 1940 in Pennsylvania; and the following authors of chapters of the book, "The Ring-Necked Pheasant and its Management in North America" (McAtee *et al* 1945): Sharp and McClure in Nebraska and Pearce in the Northeast).

Other writers have cast some doubt on the distinct boundaries of pheasants' territories. Leedy and Hicks (McAtee *et al* 1945, p. 64) wrote:

"Observations in Ohio indicated that such territories (as those described by Wight 1933) are not always clearly defined, although . . . the range of individual males and females may not be more than a few acres."

In this connection, Leffingwell (1928, p. 12) wrote that the exact amount of territory which one male will defend is unknown. He suggested that this

could best be studied in a locality where the maximum number of pheasants occurred, as when fewer are found, the limits of each one's ground are hard to define.

In the Winnebago investigation, comparatively high pheasant densities proved to be of little help in delineating definite crowing areas. The following event illustrates the difficulty in assigning fixed boundaries to them: On April 6, 1939, five females were observed travelling westward. In succession they crossed a meadow, a narrow slough with borders running north and south, and passed into a corn stubble field. While the females were at the east edge of the slough, one of them went southward. A male appeared from the south part of the meadow, approached her, and began to display. Another male ran from the westward toward the first male, whereupon the first male ran northward, then eastward, retreating well back into the meadow. The second male next walked toward the group of four females, then approached the one female in the slough. As he neared the slough, the first male returned and chased him far to the westward, then came back and consorted with the females as they all journeyed westward into the stubble. In this case, the slough at first seemed to constitute a boundary between territories, but first one male, then the other, seemed to yield ground from it.

The episode described in the preceding paragraph might be attributed to early adjustment of territories, but cases like it were observed until mid-May when establishment of nests was at its height. Even after that time, limited observations did little to clarify territorial boundaries. Throughout spring, there were numerous cases in which a field which the observer had come to regard as the domain of a particular male was traversed by another male without apparent strife resulting. Changes in field layout such as plowing of weedy oats stubble seemed to result in frequent shifting of the promenade grounds of individual males, as did the growth of crops each spring.

As compared to studies in Michigan and in the Northeast, the Winnebago investigation doubtless dealt with generally higher pheasant densities, larger fields, and fewer natural boundaries in the form of brushy fence rows, etc. It is quite possible that to these differing conditions can be attributed some differences in interpretation of territorial behavior among the pheasants. Whatever the reason, the writer was unable to map crowing areas or territories except in two or three questionable cases. The opinion derived was that under the conditions of the Winnebago Area, there probably was a tendency toward the establishment of crowing areas or territories by the male pheasants, but that these territories were very plastic and subject to frequent readjustments, probably even through the nesting phase.

THE FUNCTION OF FIGHTING

If the crowing areas are actually territories according to Noble's (1939) definition of a territory

as "any defended area," then some fighting must be over territory. Leffingwell's (1928) view was that fighting is a defense of territory. Wight's writings are confusing on this point. The general impression given by his works, that fighting is a defense of area, is contradicted by his statement (Wight, 1933) that rivalry among cocks seems to be over the female and not territory, although territories probably selected by the hens are protected by the males. In McAtee *et al.*, 1945, Wight wrote (p. 172):

"The cocks fight over the possession of hens. . ."

In the Winnebago investigation, it appeared that most fighting was over area and not females, but the presence of females usually precipitated conflicts. Before the onset of nesting, the females wandered from one area to another, and fighting between males often resulted if one male trespassed upon another's domain while consorting with hens. If a male flew or ran into another's area and attempted to copulate with a female therein, or if a male which was flushed by the observer flew into another's domain, a fight or a chase usually developed. A few conflicts observed may have been over females and not area; the presence of territorial fighting need not preclude conflicts from other causes. Despite this possibility and despite the variation in defended boundaries, fighting appeared to be caused mostly by attempted intrusions.

SELECTION OF NESTING SITES

Whether the female pheasant freely selects a nesting site or whether she is at least limited in her choice of a place by territorial restrictions recognized by the male is a question in need of clarifying. On this point Wight (McAtee *et al.* 1945 pp. 146-147) stated that the hens chose the nesting sites, and (p. 173) that the nests are within or near the crowing area. Kendeigh (1941) studied territoriality among prairie birds in northwest Iowa from early June to August, 1940. Of the pheasant, he wrote that the regular spacing of the nests suggested territoriality at an earlier period. Randall (1940a) and Leedy and Hicks (McAtee *et al.* 1945) suggested that the observed grouping of nests in certain fields might be related to boundaries of crowing areas. Sharp & McClure (McAtee *et al.* 1945) wrote of a "crowing and nesting territory," apparently regarding it as one unit.

The plasticity of crowing areas under conditions of the Winnebago investigation rendered it impossible to determine an exact relationship between territorial boundaries and placement of nests, if such relationship existed. Males were frequently flushed near laying and incubating hens and there were some signs that nests were included in defended areas. A condition described by Hochbaum (1944) for river ducks, in which the nest was outside the territory probably does not apply to pheasants.

In 1941, the writer found 20 pheasant nests in a red clover field of 11.8 acres when the field was mowed. Earlier in the spring, several male pheasants had been seen feeding and courting in a plowed

field just to the south of the clover and in road ditches bordering it, but few cocks had been seen actually in the hayfield. Indications were that as the hay grew, the hens found it attractive for nesting, and the males adjusted their territories to include it. Whether the males did their adjusting just before or after the hens started nesting in the field, it is impossible to state.

It is thought that nests were located in defended areas, but that the choice of nesting sites probably rested with the hens and was related more strongly to availability of cover and cover preferences than anything else, the males perhaps adjusting their territories to include nests.

SIGNIFICANCE OF TERRITORIES IN PHEASANTS

Wight (McAtee *et al.* 1945) wrote that other things being equal, the population of pheasants on a given area will be proportional to the number of crowing areas and that this number in turn is determined by the frequency and density of brushy cover. In an earlier publication Wight (1933) suggested management plans for increasing the number of crowing areas. These plans included protection of fence rows, protection of woodlots from grazing, and protection of kettle holes from cutting, burning, and grazing, etc. Pearce (McAtee *et al.* 1945) wrote that in the Northeast, scarcity of crowing territories rarely limits reproduction, one reason apparently being that pheasant densities are generally low enough there to leave some available areas unoccupied.

From 1939 to 1941, the breeding populations of pheasants on the Winnebago Area almost tripled without any changes in farm layout conducive to the formation of more crowing areas. Early each spring males were often seen in or near plum thickets, willow thickets, farm groves, and to lesser extent in the rather meager herbaceous growth remaining from the previous year in pastures, road ditches, stubble fields, and the like. Hayfields, which Wight (McAtee *et al.* 1945) regarded as insufficient shelter for crowing areas until late June, seemed adequate on the Winnebago Area by mid-May. Invariably there were at least some nests in large fields of suitable nesting cover, no matter how barren the fields and their surroundings had been in April. Apparently the males were able to establish territories in growth of the year before lack of early cover could seriously handicap reproduction. Even with the high populations present in 1941, there was some reason to believe that still more crowing areas could have been established in certain fields.

It is difficult for the writer to imagine that lack of suitable interspersed brushy cover or its like for establishment of crowing areas could possibly have been a limiting factor in reproduction of pheasants on the Winnebago Area. This sort of cover seemed helpful but not essential; in its absence, the birds mated and nested quite successfully.

Territorial competition among pheasants as affected by their own densities rather than by cover

arrangement may have considerable effect on pheasant reproduction. Of this possibility, Einarsen (1945) wrote (p. 5):

"It is very probable that territorial competition among the birds adversely affected reproduction. Cock birds have been seen persistently molesting hens and chicks. As the population increased, single eggs dropped at random were frequently found. Hen pheasants established community nests which resulted in many wasted eggs, as no attempt was made to incubate them. . . . This did not occur when pheasant populations were smaller."

In the Winnebago investigation, single eggs and community nests were observed during all three years. In 1941, when nesting density was highest, greater numbers (not completely recorded) of single eggs were found, and a slightly higher proportion of community nests was observed than in the other two years, but the total numbers of community nests were not great enough to demonstrate a significant difference. In 1941, hens were found nesting more frequently in "odd" places like manure piles and straw stacks (Figure 6), and this sort of behavior is possibly symptomatic of crowding.

Errington (1945) put forward an hypothesis that depression phases in reproduction and survival might be brought on by a dominant agency through modifications of ordinary limits of intraspecific toleration. If this hypothesis proves to be valid, territorial mechanisms of some sort might have considerable effect upon population trends, but probably not in ways easily controlled through environmental manipulation.

In summary, the Winnebago investigation demonstrated beyond doubt that certain males tended to reappear in the same general localities in the spring. Crowing areas were thought to be defended by the males, but were very plastic. Fighting was mostly a defense against intrusion rather than direct competition for females, but in a few instances may have started over hens. Nest sites were probably defended by males, which may have readjusted their territories to include the nests. Lack of suitable cover for crowing areas could scarcely have limited pheasant reproduction, but territorial competition of an indirect sort influenced by density may have had some such effect. The knowledge of territoriality among pheasants under conditions of high densities, large fields, and few natural boundaries could probably be greatly furthered by an intensive study of this phase alone if great numbers of birds were marked. The writer marked several pheasants according to Trippensee's (1941) method, but the only markers seen again had come off the feathers.

SEX RATIO

The male/female ratios of the breeding population in this investigation were estimated to be as follows: 1939, 1:2.4; 1940, 1:2.1; 1941, 1:2.0. It is unlikely that these ratios adversely affected fertility of eggs for Randall (1939) found 94.1% of the pheasant eggs fertile during his investigation, and the sex ratio

was six females to a male. The percentage of fertility found in the Winnebago investigation was about 92%. In Ohio, Hicks & Leedy (McAtee *et al* 1945) reported an average springtime percentage of males (over a three year period) of 27, which equals one male to 2.7 females, and the fertility of eggs was 92%.

NESTING HABITS

DATES OF LAYING

The earliest nests found were established in the following bi-monthly periods: 1939, April 16-30; 1940, April 1-15; and 1941, March 16-31. The earliest nest found was probably established about March 20, 1941; however, it was not found until mid-April and the exact date it was started is a matter of conjecture. In 1939, the last nest found was established between July 16 and 31; in 1940, between August 1 and 15; and in 1941, July 16-31.

CONSTRUCTION OF NESTS

The nests were constructed essentially as described by Hamerstrom (1936), generally consisting of a scooped out natural depression, four to seven inches in diameter and from one to three inches deep at the center. There was usually little or no lining under the first egg, but an accumulation of plant debris and down feathers appeared as new eggs were laid. In incubated nests the lining was 0.25 to 1.5 inches thick. All sorts of plant materials were used in the linings, and their choice seemed to be determined by availability. Sometimes no bowls were present. In small grain, for example, the lining was often an elevated platform suspended from the butts of living plants, with the entire nest above the earth. As Hamerstrom (1936) observed, any concealment by roofing appeared accidental.

EGG-LAYING

Eggs were laid generally during the interval between the two daily feeding periods, that is, in the period starting about two hours after sunrise and ending about two hours before sunset.

In "normal" nests the rate of laying was slightly less than one egg per day. However, it is not uncommon for more than one pheasant hen to contribute to a clutch. At least three hens may lay in a single nest and consequently the rate of appearance of eggs in such nests may be three per day or higher. In the first nest found during 1939, ten eggs were laid in five days, and during one day, three new eggs appeared (Figure 4). Clutches to which two or more females have contributed are called "compound sets" or "dump nests." Tremendous clutches sometimes occur and the record for this investigation was 31 eggs, equalling the greatest number found by Hamerstrom (1936) in northwest Iowa. The phenomenon of plural use of nests has been observed among other gallinaceous species, including the bobwhite (Stoddard 1931). Pheasants have been known to lay eggs in the nests of many other ground nesting species (Tegetmeier 1904), and in northwest Iowa,



FIG. 4. "Dumpnest" or "Compound Set" with 25 Eggs in Nest.

Bennett (1938) reported that 4.7 per cent of 341 nests of the blue-winged teal (*Anas discors*) were parasitized by the pheasant. In the Winnebago investigation, the following cases of inter-specific nesting parasitism were observed: (1) three European partridge nests with pheasant eggs, (2) one pheasant nest with two partridge eggs, and (3) one pheasant nest with a chicken egg.

In common with many other game birds, pheasants drop single eggs promiscuously, particularly in the early part of the breeding season. In the case of the bobwhite, Stoddard (1931) regarded such eggs as indicative of nest-destruction, or failure of the female to reach the nest in time. During the season of 1941, when 318 nests were found, 74 single eggs were recorded. "Singles" were sometimes placed in scooped out bowls, but usually there appeared to have been little preparation for their deposition.

INCUBATION

Female pheasants may often lay an egg or two after having begun incubation. Many hatched nests



FIG. 5. Hatched Pheasant Nest in Slough Border with Three Eggs not Hatched.



FIG. 6. Pheasant Hen Incubating in Strawstack.

contained unhatched eggs with embryos which had died one, two, or three days before hatching, indicating that the other chicks had hatched and the females had left their nests before these later chicks could pip the egg (Fig. 5). The probability that these delayed eggs were laid later than the others was borne out by examination of sets of eggs from incubated nests which were destroyed. In these eggs, also, most of the embryos were at the same stage but a few were one, two, or three days retarded.

Though the incubation period varied somewhat in the field, it was found to be about 23.5 days when pheasant eggs were placed under chicken hens.

REST PERIODS

Leopold (1936) gave "dawn and 4:00 P.M." as the times at which incubating pheasant hens leave the nests or take "rest periods." In the Winnebago investigation, one nest was visited 37 times at hours ranging from 4:15 A.M. until 7:05 P.M., and the female was off the nest only three times: once at 7:05 A.M., and again at 6:35 A.M. on another day, and again at 7:50 A.M. on still another day. No definite times were discovered at which the writer could predict with accuracy that any individual female would be away from the nest.

DESERTION

Desertion as a source of nesting loss is discussed elsewhere in this paper.

In agreement with other observers (Leopold 1936),

it was found that desertion is more likely to occur when the female was disturbed at the nest before incubation had begun and that likelihood of desertion lessened as incubation proceeded. However, no completely "safe" period was found to exist. In some instances, desertion of pipped eggs was recorded following violent disturbances.

The manner of approach by the observer made some difference in the flushing behavior of the females when they were laying or incubating. When the observer saw an incubating hen even almost underfoot, if he kept on walking and made no sudden moves, the female usually did not flush; if he stopped nearby or returned to the nest immediately the bird often did flush. Mosby & Handley (1943) found that the observer's manner of approaching a nesting turkey hen made considerable difference in the likelihood of flushing her. Some pheasant hens acquired a "flushing habit" and flew if a man walked near them. Others allowed the observer to touch them repeatedly with the hand, although the utmost caution was used to prepare them for this act. In general, hens which had been flushed and returned were more likely to flush again than females which had never been flushed from their nests by the observer.

CARE OF YOUNG

After most of the eggs are hatched, the females and their broods stay in the nests or close to them for several hours. In case of disturbance by man, predators, or machinery, the female may move the chicks as quickly as they are capable of locomotion.

The females usually stay with their broods until the chicks are at least six to eight weeks old. Males seem to take little responsibility in the rearing of the young, although twice during the investigation, cocks were observed accompanying chicks of three or four weeks when no females were seen in the vicinity. Leffingwell (1928) observed males with six or seven week old chicks when no female was present.

After the chicks have reached the age of seven or eight weeks there is a tendency for the broods to assemble (Errington and Hamerstrom, 1937). Assemblages of broods, often with adult females, are to be seen late in the summer and early in the autumn. At this time, most of the young are assuming adult plumage.

LOCATION OF NESTS

The maps (Figures 1, 2, and 3) show the locations of nests on the 1,520-acre plot, and Tables 2, 3, and 4 summarize the information collected on location of nests during the three years. Any apparent discrepancies between this presentation of the 1939 data and that of the earlier paper (Baskett, 1941) result from reclassification of nesting data and cover types to facilitate comparison of information for all three years.

The land of the Winnebago Area is intensively farmed and pheasants are forced to find nesting

places mostly on agricultural land. Because agricultural treatments of different types of cover have considerable effect on the fates of nests therein, the main headings in Tables 2, 3, and 4, were designed

TABLE 2. Acreages, Nesting Densities, and Nesting Success, 1939.

Cover Type	Acreages	Number of nests	Percentage of all nests	Acres per nest	Number of nests successful	Percentage of nests successful
I. Hayfields	212.9	26	34.67	8.2	9	34.6
A. Alfalfa.....	37.8	6	8.00	6.3	1	16.6
B. Alfalfa and sweet clover.....
C. Alfalfa and timothy.....
D. Timothy.....	5.6
E. Quack grass.....	5.6
F. Native grasses (meadows).....	68.3	7	9.33	9.8	1	14.3
G. Native grasses and mixed herbaceous (road ditches).....	20.4	7	9.33	2.9	3	42.9
H. Canary grass.....	23.8	6	8.00	4.0	4	66.7
I. Oats hay.....	48.2
J. Bluegrass and red clover.....	2.2
K. Red clover.....
L. Sweet clover ^a
M. Sudan grass.....	1.0
II. Small grains and flax	443.7	15	20.00	29.6	12	80.0
A. Oats.....	378.9	13	17.33	29.1	10	76.9
B. Barley.....	37.3	2	2.67	18.6	2	100.0
C. Flax.....	17.5
D. Flax and sweet clover.....	10.0
III. Pastures	206.5	8	10.67	25.8	1	12.5
A. Bluegrass.....	124.2	2	2.67	62.1
B. Brome grass.....	20.3
C. Canary grass.....	19.5	3	4.00	6.5	1	33.3
D. Quack grass.....
E. Oats.....	3.9
F. Native grasses.....	22.8	2	2.67	11.4
G. Quack grass and mixed weeds.....	7.5
H. Sudan grass.....
I. Alfalfa.....	2.9
J. Sweet clover.....	5.4	1	1.33	5.4
IV. Corn and cane	456.0
A. Corn.....	452.7
B. Cane.....	3.3
V. Manure crops	10.5
A. Oats.....
B. Sweet clover.....	10.5
VI. Other crops	42.7
A. Soybeans.....	30.8
B. Beets.....	11.9
VII. Indirect or non-agricultural use	147.7	23	30.67	6.4	5	21.7
A. Fence rows.....	7.8	19	25.33	.4	4	21.1
B. Sloughs.....	14.5	3	4.00	4.8
C. Roads and lanes.....	20.5
D. Gravel pit.....	0.1
E. Idle.....	48.4	1	1.33	48.4	1	100.0
F. Farm groves and feed lots.....	52.4
G. Straw stacks.....	0.1
H. Gardens.....	3.9
VIII. Miscellaneous early cover later removed	(56.2)	3	4.00	18.7
Totals	1520.0	75	27	36.0

^aMowed early to improve stand for seed production.

to suggest general agricultural treatment. The subheadings, however, name the principal crop plants or suggest the type of native vegetation or the physical nature of a place where nests were found if no plant cover was present. In case a crop was so

TABLE 3. Acreages, Nesting Densities, and Nesting Success, 1940.

Cover Type	Acreages	Number of nests	Percentage of all nests	Acres per nest	Number of nests successful	Percentage of nests successful
I. Hayfields.....	212.6	64	45.71	3.3	13	20.3
A. Alfalfa.....	65.8	26	18.57	2.5	4	15.4
B. Alfalfa and sweet clover.....	13.7
C. Alfalfa and timothy.....	12.9
D. Timothy.....
E. Quack grass.....	7.0
F. Native grasses (meadows).....	58.5	9	6.43	6.5	3	33.3
G. Native grasses and mixed herbaceous (road ditches).....	20.4	12	8.57	1.7	1	8.3
H. Canary grass.....	22.8	13	9.29	1.8	4	30.8
I. Oats.....	2.9
J. Bluegrass and red clover.....	2.3
K. Red clover.....
L. Sweet clover*.....	6.4	4	2.86	1.6	1	25.0
M. Sudan grass.....
II. Small grains and flax.....	478.4	32	22.86	15.0	13	40.6
A. Oats.....	405.4	30	21.43	13.5	13	43.3
B. Barley.....
C. Flax.....	73.0	2	1.43	36.5
D. Flax and sweet clover.....
III. Pastures.....	208.1	10	7.14	20.8	4	40.0
A. Bluegrass.....	129.6	3	2.14	43.2	1	33.3
B. Brome grass.....	22.1	4	2.86	5.5	2	50.0
C. Canary grass.....	19.5
D. Quack grass.....
E. Oats.....	3.9
F. Native grasses.....	22.8	3	2.14	7.6	1	33.3
G. Quack grass and mixed weeds.....
H. Sudan grass.....
I. Alfalfa.....	10.2
J. Sweet clover.....
IV. Corn and cane.....	426.1
A. Corn.....	422.9
B. Cane.....	3.2
V. Manure crops.....	18.5
A. Oats.....	7.4
B. Sweet clover.....	11.1
VI. Other Crops.....	65.0	1	.71	65.0
A. Soybeans.....	65.0	1	.71	65.0
B. Beets.....
VII. Indirect or non-agricultural use.....	111.3	30	21.43	3.7	5	16.7
A. Fence rows.....	7.9	23	16.43	.3	3	13.0
B. Sloughs.....	14.4	2	1.43	7.2	1	50.0
C. Roads and lanes.....	20.7
D. Gravel pit.....	0.1	1	.71	.1	1	100.0
E. Idle.....	11.3
F. Farm groves and feed lots.....	52.6	4	2.86	13.2
G. Straw stacks.....	0.1
H. Gardens.....	4.2
VIII. Miscellaneous early cover later removed.....	(10.0)	3	2.14	3.3
Totals.....	1520.0	140	35	25.0

*Mowed early to improve stand for seed production.

contaminated with the growth of another plant that the nature of the cover was greatly affected, the names of both plants are listed in the subheadings (see Item I-B, Tables 2, 3, and 4).

In order to characterize the cover types further

TABLE 4. Acreages, Nesting Densities, and Nesting Success, 1941.

Cover Type	Acreages	Number of nests	Percentage of all nests	Acres per nest	Number of nests successful	Percentage of nests successful
I. Hayfields.....	275.3	206	64.78	1.3	42	20.4
A. Alfalfa.....	57.4	31	9.75	1.9	3	9.7
B. Alfalfa and sweet clover.....	15.8	3	.94	5.3
C. Alfalfa and timothy.....	18.0	6	1.89	3.0
D. Timothy.....
E. Quack grass.....	3.6
F. Native grasses (meadows).....	58.7	25	7.86	2.3	10	40.0
G. Native grasses and mixed herbaceous (road ditches).....	20.4	48	15.09	.4	19	39.6
H. Canary grass.....	30.2	35	11.01	.9	4	11.4
I. Oats.....	22.3	2	.63	11.2
J. Bluegrass and red clover.....	2.2	2	.63	1.1
K. Red clover.....	25.5	40	12.58	.6	6	15.0
L. Sweet clover*.....	21.2	14	4.40	1.5
M. Sudan grass.....
II. Small grains and flax.....	461.1	62	19.50	7.4	25	40.3
A. Oats.....	420.8	61	19.18	6.9	24	39.3
B. Barley.....
C. Flax.....	40.3	1	.31	40.3	1	100.0
D. Flax and sweet clover.....
III. Pastures.....	224.5	8	2.52	28.1	3	37.5
A. Bluegrass.....	110.7	3	.94	36.9	1	33.3
B. Brome grass.....	22.1	3	.94	7.4	1	33.3
C. Canary grass.....	19.5
D. Quack grass.....	3.4	1	.31	3.4	1	100.0
E. Oats.....	25.2
F. Native grasses.....	22.8
G. Quack grass and mixed weeds.....
H. Sudan grass.....	0.6
I. Alfalfa.....	6.6
J. Sweet clover.....	13.6	1	.31	13.6
IV. Corn and cane.....	430.0
A. Corn.....	427.1
B. Cane.....	2.9
V. Manure crops.....	6.6	2	.63	3.3	1	50.0
A. Oats.....
B. Sweet clover.....	6.6	2	.63	3.3	1	50.0
VI. Other crops.....	24.3
A. Soybeans.....	24.3
B. Beets.....
VII. Indirect or non-agricultural use.....	98.2	31	9.75	3.2	3	9.7
A. Fence rows.....	8.1	21	6.60	.4	1	4.8
B. Sloughs.....	14.0
C. Roads and lanes.....	20.7
D. Gravel pit.....	0.1
E. Idle.....	6.2	1	.31	6.2
F. Farm groves and feed lots.....	48.9	6	1.89	8.2	1	16.7
G. Straw stacks.....	0.2	3	.94	.1	1	33.3
H. Gardens.....
VIII. Miscellaneous early cover later removed.....	(67.1)	9	2.83	7.5
Totals.....	1520.0	318	74	23.2

*Mowed early to improve stand for seed production.

and to explain briefly the relationship of agriculture to pheasant nesting in some kinds of crops, the more important varieties of cover are discussed topically.

HAYFIELDS

During the three years hayfields contained over half (55.6 per cent) of all nests found, and nearly half (47.0 per cent) of all successful nests; nevertheless, the rate of loss in hayfields was rather high, with only 21.6 per cent succeeding. These findings agree closely with those of English (1933) and Randall (1940) who searched intensively for nests.

On the basis of figures which showed higher densities of hayfield nests in thickly populated areas, Leopold (1937) suggested that heavy hayfield nesting occurs only where the other (and preferred) cover does not suffice to accommodate more than a part of the population. Randall's (1940) findings tended to support this hypothesis.

The Winnebago data demonstrated a striking proportional increase in hayfield nests with denser populations, and conversely, lower proportions of nests in fence rows as density increased. (See Table 5). The systematic and intensive search for nests gives these relations undeniable validity.

TABLE 5. Relationships of Hayfield and Fence Row Nesting to Breeding Densities.

Year	Breeding densities (Pheasants/sq. mile)	Nests located in hayfields*	Nests located in fence rows
1939.....	50	19 or 25.3%	19 or 25.3%
1940.....	80	52 or 37.2%	23 or 16.4%
1941.....	125	158 or 49.7%	21 or 6.6%

*Nests in road ditches not included.

The writer concurs with Leopold's (1937) hypothesis relative to hayfield nesting. Fence rows were apparently saturated with nests all three years, for the total numbers of nests in them did not rise appreciably in 1940 or 1941; heavy use of fence rows through preference or necessity or likely both, is thereby indicated. With the greater densities of 1940 and 1941, an increasing proportion of pheasants was probably forced into less attractive cover, of which hayfields constituted a major part. The same principle may apply to crowing areas, whatever the relation of these areas to nest sites. Males may prefer to include brushy cover, weedy fence rows and the like in their territories, but where populations are high many of them may be forced to accept areas entirely within growth of the year as it becomes available.

ALFALFA

Alfalfa was consistently a much-used type of cover, with from 8.0 per cent (1939) to 18.6 per cent (1940) of all nests located in it. Relatively few nests (9.7 to 16.6 per cent) were successful in alfalfa as it was generally the first hay crop to be mowed. The first mowing started about June 15, although one field was cut on June 7, 1941. No new nests were found during the second cutting of

alfalfa in any year. Various other plants contaminated alfalfa stands at least slightly; notable among these were wild barley (*Elymus canadensis*), and bluegrass (*Poa pratensis*).

NATIVE GRASSES (MEADOWS)

Hay meadows did not contain nests in such high densities as did certain other types of hay crops but the later mowing, generally begun about June 25, permitted higher proportions of the nests to reach completion. Various prairie grasses, including particularly the big and little bluestems (*Andropogon furcatus* and *A. scoparius*), and Indian grass (*Sorghastrum nutans*) were found here. Many native forbs were found in the meadows, and several exotic species occurred in small numbers. Marsh border plants, including sedges (*Carex* spp.) and smartweeds (*Polygonum* spp.) were generally avoided in haying.

During the three years, 14 nests in meadows hatched, as compared to eight in alfalfa.

ROAD DITCHES

Road ditches grew up to many kinds of plants, including both native and exotic species. Among the most numerous were the bluestems (*Andropogon scoparius* and *A. furcatus*), many species of the Compositae, including goldenrods (*Solidago* spp.), and the ragweeds (*Ambrosia* spp.), sweet clover, timothy, squirrel's tail (*Hordeum jubatum*), Kentucky bluegrass and quack grass (*Agropyron repens*). Ditches beside different roads exhibited little similarity in plant cover, but they did have in common their narrow shapes and their proximity to open roads. These latter characteristics probably have some relation to the use of the ditches as nesting sites. Road ditches were usually mowed in late June and July. (See Figure 7.) During the three years, they contained 23 nests which hatched.

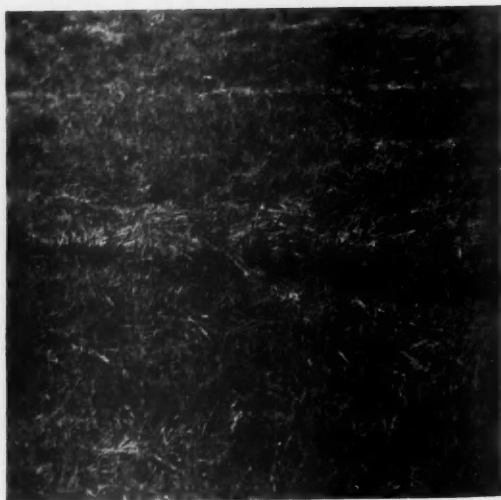


FIG. 7. Pheasant Female on Nest in Mowed Road Ditch.

CANARY GRASS

Hayfields of reed canary grass (*Phalaris arundinacea*) afforded very dense cover by the first of June and were attractive to the nesting pheasants. Mowing of canary grass generally followed that of alfalfa, occurring late in June.

Nests in canary grass showed an over-all success of 22.2 per cent for the three years, as compared to 12.6 per cent for nests in alfalfa. Canary grass, a very productive hay for peaty soils of the area, seemed to hold some promise of balancing out losses in other types of hay. However, the striking nesting successes in sweet clover seed fields reported by Strode and Leedy (1940) and in alsike clover seed fields reported by Strode (1941) as occurring in Ohio were not approached in any type of cover on the Winnebago Area, when significant numbers of nests were concerned.

RED CLOVER

Dense pure stands of red clover were grown on the 1,520-acre plot only in 1941, and 40 pheasant nests were found in 25.5 acres of this cover. Except for fence rows and road ditches, red clover contained the highest densities of nests recorded. Mowing was begun on June 19, 1941; 15 per cent of the nests were successful.

SWEET CLOVER

In 1940 and 1941, a few stands of sweet clover were clipped early in June in an attempt to give the plants a more bushy form, facilitating the harvesting of seeds. Although the plants were not used as hay, the fields are classified under "hayfields" because of the similarity of agricultural treatment.

In Ohio, Strode & Leedy (1940) reported that 42.3 per cent of all pheasant nests studied during 1939 were in fields of sweet clover cut late for seed. These fields occupied only three per cent of the area. Nesting success was great, 87.4 per cent of the nests in sweet clover producing chicks. In the Winnebago investigation, densities of nests in sweet clover were high, comparing favorably with those in alfalfa, for example, but were never extremely high. Nesting success in sweet clover did not exceed 25 per cent, a fact probably related to the practice of clipping the clover in June.

SMALL GRAINS

OATS

In oats fields, the nesting densities were low, but percentages of success of nests were high. In 1939, 44.4 per cent of all productive nests were located in oats; in 1940, 37.1 per cent; and in 1941, 32.4 per cent. Fields of small grains ranked second only to hayfields in total production of chicks.

Oats cover did not become available for nesting cover until June, and it is probable that many females, evicted from nests in hayfields, moved into oats for the next nests. Harvesting of oats was begun earliest in 1939, when one field was cut on



FIG. 8. Harvested Oats Field on Winnebago Area.

July 10, but it usually proceeded during the time from July 13 to July 24.

PASTURES

Most pastures were heavily grazed, and relatively few nests were found in them. The pastures containing the largest numbers of nests were those on which cover was most dense.

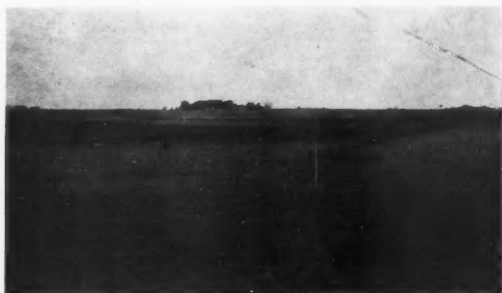


FIG. 9. Heavily Grazed Bluegrass Pasture.

CORN

No nests were found in fields of growing corn, but a few were located in old corn fields at the bases of the corn plants, and usually in growth of foxtail (*Setaria* spp.). All known nests so located were destroyed by predation or by farm machinery when the fields were disked.

MANURE CROP—SWEET CLOVER

Sweet clover left undisturbed throughout the summer was not found to contain many nests, but in the dense growth of the plant it was very difficult to find the later nests.

NON-AGRICULTURAL

FENCE ROWS

Fence rows exhibited little similarity to one another with reference to plant cover present. Some of these strips had some native plants of the prairie, including wild rye (*Elymus canadensis*), slough grass (*Spartina Michauxiana*), and many other grasses and forbs. Some rows were grown up to greater ragweed (*Ambrosia trifida*), whereas others

had nearly pure stands of sweet clover, bluegrass, and various other exotics.

Although fence rows constituted only a tiny part of the acreage of the nest-study area, from 6 to 25 per cent of the nests were found in them. Many nests located in the fence row strips were early, and were begun when a high proportion of ground vegetated at the time was in fence rows (Figures 10, 11, and 12). Few nests were successful in this cover, for they suffered heavily from predation and desertion, as did most of the early nests.

PERIPHERAL LOCATION

Wight (1930), English (1933), and Hamerstrom (1936) found evidences of a tendency for pheasants to place their nests at least proportionally near edges, but Leopold (1937) and Leedy (1938) found no such indications. Leopold (1937) suggested that crowding of nests might force the birds to accept non-peripheral locations, and Randall (1940) found the percentage of nests away from peripheries increasing as nesting density increased.

On the Winnebago Area nesting populations in-

creased from about 50 pheasants per square mile in 1939 to 80 in 1940, and about 120 to 130 in 1941. In 1939, 48.6 per cent of all nests were located in fields with a minimum dimension greater than 200 feet ("field nests"); in 1940, 67.1 per cent of all nests were field nests; and in 1941, the percentage was 68.5. The remaining nests were in narrow strips of cover such as fence rows, road ditches, and narrow extensions of fields, all of which might well be considered peripheral in location. Therefore, a general tendency away from peripheral placement of nests as nesting density increased was indicated. However, the locations of the field nests within their fields did not clearly indicate such a tendency (see Table 6).

NESTING LOSSES

In common with other ground-nesting birds, pheasants suffer very heavy losses of nests. The highest published percentage of success for a large series of pheasant nests found in varied types of cover is 58.4 per cent (Strode and Leedy, 1940). Generally, nesting studies have shown a much lower



FIG. 10. Early Fence Row Cover.



FIG. 11. Early Fence Row Cover.



FIG. 12. Early Nest in Fence Row.

TABLE 6. Locations of Field Nests with Respect to Peripheries.

Year	Distance to nearest vegetation type-line	Percentage of field nests
1939.....	Less than 50 feet	40
	Less than 100 feet	57
1940.....	Less than 50 feet	29
	Less than 100 feet	52
1941.....	Less than 50 feet	30
	Less than 100 feet	58

proportion of productive nests. In the Winnebago investigation, percentages of success were as follows: 1939, 36.0 per cent; 1940, 25.0 per cent; and 1941, 23.2 per cent.

All nests from which no chicks departed were considered unsuccessful, and conversely, all nests from which at least one chick departed were termed successful.

CAUSES

The causes of losses of nests are summarized in Tables 7 and 8. An attempt at strict cataloguing of these causes is arbitrary for two principal reasons: (1) the agent bringing about failure of an individual nest is difficult to determine with certainty in the field, and (2) many of the causes are closely interrelated. For example, removal of hay by mowing is often followed by heavy predation upon nests exposed. Furthermore, it is often impossible in such cases to determine whether the female had deserted the nest before the predator had arrived. Whenever distinctions could be made, losses were listed under primary causes.

Failures of half of the unsuccessful nests were traceable to desertion (Item II, Table 8), and by far the most fatal specific cause was desertion following disturbance to female, nest, or cover, by agricultural activities, which accounted for 31.2 per cent of all losses (Item IIC, Table 7). In most cases this disturbance occurred during haying and harvesting, at which times nests were smashed, females were injured or killed, or else often deserted the nests as a reaction to the presence of the farmers or the exposure of their nests.

TABLE 7. Causes of Nest Destruction.

Cause of loss	1939	1940	1941	Totals	Percentages of all unsuccessful nests
I. Unknown.....	..	2	3	5	1.3
II. Desertion because of:					
A. Dump nests and nesting parasitism.....	1	1	5	7	1.8
B. Observer.....	5	5	10	20	5.1
C. Disturbance of hen, nest, or cover by agricultural activities.....	10	28	84	122	31.2
D. Disturbance of female by grazing animal.....	1	1	0.2
E. Disturbance by predator.....	1	1	0.2
F. Flooding.....	1	1	..	2	0.5
G. Unknown causes.....	5	8	33	46	11.8
III. Predation by:					
A. Crow (certain).....	2	18	18	38	9.7
B. Crow (probable).....	5	18	13	36	9.3
C. Unknown bird.....	1	1	0.2
D. Ground squirrel.....	..	1	..	1	0.2
E. Hog.....	..	2	1	3	0.8
F. Skunk.....	1	..	2	3	0.8
G. Weasel.....	1	1	0.2
H. Mink.....	1	1	0.2
I. Weasel or mink.....	1	1	0.2
J. Cat.....	4	4	1.0
K. Unknown carnivore.....	5	2	20	27	6.9
L. Man.....	1	..	1	2	0.5
M. Unknown mammal.....	..	2	5	7	1.8
N. Unknown animal.....	2	5	15	22	5.6
IV. Physical injury to female by farm machinery.....	2	8	17	28	7.2
V. Mortality of female from:					
A. Predation.....	..	1	2	3	0.8
B. Farm machinery.....	1	1	7	9	2.3
Totals.....	45	103	243	391	100.0

TABLE 8. Summary of Causes of Nest Destruction.

Causes	1939	1940	1941	Totals	Percentages of all unsuccessful nests
I. Unknown.....		2	3	5	1.3
II. Desertion.....	23	43	133	199	50.8
III. Predation.....	18	48	81	147	37.6
IV. Physical injury to female by farm machinery.....	3	8	17	28	7.2
V. Mortality of females.....	1	2	9	12	3.1
Totals.....	45	103	243	391	100.0

Desertion generally followed when pheasant nests were parasitized, although one nest containing 26 eggs, perhaps a "dump nest," was incubated. For numerical data on causes of losses, nests were classified as "dump nests" only when the rate of laying was known, or when numbers of eggs were very high and the eggs were carelessly piled and scattered (see Figure 4).

Desertion of nests were accredited to the observer whenever he flushed the females and the nests remained inactive thereafter. Failure so classified amounted to 5.1 per cent of all losses.

Flooding was a minor cause of failure, and caused losses of only two nests during the three nesting seasons. One flooded nest was located in a slough, and was inundated after a very heavy rain. The female was incubating, and remained upon the nest long after it was completely covered with water. The other was located on a road bank and was washed by a stream of water which poured off the road during a cloudburst.

Predation was a serious cause of nesting failure, having accounted directly for losses of 37.6 per cent of all unsuccessful nests.

Crows committed the greatest numbers of depredations and were especially active in their pilfering during the early part of the pheasant nesting season and following removal of cover by mowing and harvesting. In Table 7, crow depredations appear under two classifications. Those appearing under Item IIIA (Crow-certain), were so listed because the robbing was actually observed or eggs were found near the nest, opened in typical crow-fashion. Crows often carried the eggs far from the nests before opening them, leaving no definite evidence of their identities at the nests. One marked egg was carried one-fourth mile by a crow and then deposited. Since it was not certain that crows were responsible for disappearance of eggs from nests around which no shells were found, a separate listing (Item IIIB, Table 7) was made to segregate these cases. About three or four breeding pairs of crows hunted over the nest-research area each season, and in 1941, three crow nests were found on the area.

The rate of predation by all species was not demonstrably correlated with the total number of pheasant nests (Table 9), but it is possible that increased losses from other sources upset some such relationship. Numbers of crows and other avian

TABLE 9. Rates of Predation on Pheasant Nests in 1939, 1940, and 1941.

Year	Total number of nests found	Percentage of all nests destroyed by predation
1939.....	75	29.2
1940.....	140	41.3
1941.....	318	30.9

predators were thought not to have changed greatly from year to year, but little was known of relative numbers of carnivores present on the nest-research area during the three seasons.

Killing of females or physical injury to them by mowers and binders caused losses of only 10.3 per cent of all destroyed nests, but these losses were important, for in most cases the hens were rendered permanently incapable of reproduction (Figure 13).



FIG. 13. Pheasant Nest Mowed Over at Hatching.

During the three years' study, 296 nests were found in hayfields; in these hayfields 34 nesting females were either killed or injured by mowers. Thus, for every 100 nests found in hayfields, 11.5 hens were killed or maimed. In evaluating these losses it should not be construed that each nest located represents an individual hen, because a number of the nests were certainly re-nesting attempts. In Ohio, Strode (1941) found that for every 100 pheasant nests reported mowed over during the cutting of hay crops, farmers reported killing 39.4 hens. It is likely that the mortality indicated by Strode is in excess of that which actually existed, for farmers are much more likely to notice the nests with females on them than those without.

Other observers of pheasant nesting have attributed the heaviest losses of nest to man, largely through his agricultural activities, and to predation. Haying alone has been credited with from nearly one-third to a half of all losses (English, 1933; Hamerstrom, 1936; Randall, 1940), and in this investigation, haying was considered the primary cause in 35 per cent of nesting failures. The figure of 37.6 per cent of nests lost to predators on the Winnebago Area has generally not been equalled in other places. Hamerstrom (1936) traced 19.3 per

cent of losses to pilfering by wild animals; Randall's (1940) figure was 30.7 per cent.

LOSSES OF EGGS IN SUCCESSFUL NESTS

Often a few eggs remained unhatched in otherwise successful nests. The numbers of these eggs together with the other related data are shown in Table 10, and a summary of the causes of non-production of eggs in successful nests is presented in Table 11.

The greater proportion (73.1 per cent) of unhatched eggs of this kind failed because of delayed or imperfect hatching, and infertility or adding. As was explained previously, many of the unhatched eggs were thought to have been under-developed because they were laid after the females started incubating the others. However, it is also likely that several of the eggs included in this category were at the point of hatching when the female was forced to leave the nest. Hatching efficiency seemed somewhat lowered when the process occurred during torrential rains.

TABLE 10. Fates of Eggs in Successful Nests.

Item	1939	1940	1941
I. Total numbers of successful nests.....	27	35	74
II. Numbers of successful nests from which egg-data were available.....	27	32	66
III. Known numbers of eggs in successful nests.....	279	351	689
IV. Known numbers of hatched eggs.....	236	290	566
V. Known numbers of unhatched eggs in successful nests.....	43	61	123
VI. Average sizes of clutch in successful nests.....	10.4	11.0	10.4
VII. Average numbers of eggs hatched per successful nest.....	8.7	9.1	8.6
VIII. Average numbers of unhatched eggs in successful nests.....	1.7	1.9	1.8

In cases of partial predation, the pilferers were able to take a few eggs, probably while the hens were feeding away from the nests.

The eggs listed under "Died in early incubation," Table 11, probably came to naught because the females were kept off the nests for extended periods during very hot weather.

The only anomalous embryo found had died just before pipping, and had one eye imbedded beneath the skin, and an open brain case.

In 1939, two eggs were found infested with ants, *Lasius niger neoniger*, but since the eggs were in separate nests and as no other eggs in either nest were similarly infested, it seems probable that the chicks died in pipping and that the ants arrived following their death.

RELATIONSHIP OF LOSSES OF NESTS TO AGRICULTURAL PRACTICES

The difficulty of segregating and analyzing the causes of nesting failures was pointed out earlier.

TABLE 11. Losses of Eggs in Successful Nests.

Cause of loss	1939	1940	1941
I. Infertile or added.....	18	26	57
II. Delayed or imperfectly hatched.....	17	12	36
III. Partial predation.....	0	6	18
IV. Died in early incubation.....	0	0	6
V. Anomalous embryos.....	0	0	1
VI. Crushed by female.....	0	0	2
VII. Destroyed by observer.....	0	4	0
VIII. Failed to hatch, reasons undetermined.....	8	13	3
Total number of unhatched eggs in successful nests.....	43	61	123

However, losses of 40.7 per cent of all unsuccessful nests were traceable directly to man's agricultural activities. (See Table 7, Items IIC, IV, and VB.) The majority of these losses were attendant to mowing, harvesting, and plowing, of which operations the first two were by far the most fatal to nests.

It seems reasonable to conjecture that the relationship between the seasonal progress of pheasant nesting and of cover development and farming operations might have considerable effect upon success of nests.

The seasonal progress of farming activities and cover development are determined largely by inter-related factors of weather, and the only available quantitative data pertaining to these factors were temperature and precipitation statistics taken by a cooperator with the United States Weather Bureau at Forest City, Iowa.

An important condition determining the dates of commencing field work in the spring was ground moisture, in the poorly drained soil of the Winnebago Area. Total precipitation data from October, 1938 through April, 1939; from October, 1939 through April, 1940; and from October, 1940 through April, 1941, are given in Table 12. The periods given are for seven months preceding each nesting season, and they show considerable differences. According to the totals, the soil was wettest early in the spring of 1941, driest in 1940, and intermediate in 1939.

The dates at which preparation of fields for planting small grains, "Spring's work," was begun each year reflected in some measure the differences in accumulated soil moisture. In 1939, this work was begun by several farmers of the Winnebago Area on April 14, but unfavorable conditions forced its postponement for several days so that the work was not begun in earnest until April 19 or 20. In 1940, "Spring's work" was begun by most farmers on April 16, and was continued to completion without protracted interruption. In 1941, operations were not commenced until April 24, and even then the ground was so wet that delays were frequent.

In respect to drying of the soil and the preparation of fields for planting small grains, the spring of 1939 was "later" than that of 1940, and the spring of 1941 was "later" than that of 1939.

TABLE 12. Total Precipitation at Forest City, Iowa, October 1938 to April 1939, October 1939 to April 1940, and October 1940 to April 1941.*

Month	Total precipitation in inches		
	1938-39	1939-40	1940-41
October.....	.41	1.80	2.88
November.....	2.45	.04	3.44
December.....	1.14	.96	1.13
January.....	1.10	.97	.92
February.....	1.55	.87	1.07
March.....	.65	1.18	1.10
April.....	1.90	2.12	1.63
Totals.....	9.20	7.94	12.17

*Data taken from Reed (1938, 1939, 1940, 1941).

The average temperature at Forest City for the period from January to June, inclusive, in 1939, was 48.4 degrees F. In 1940, the average for the same period was 49.6 degrees, and in 1941, 51.3 degrees (Reed, 1939, 1940, 1941). Thus, according to average temperatures, the early parts of the growing seasons may be ranked as follows according to "earliness": (3) 1939, (2) 1940, (1) 1941.

Dates of first mowing of hay and harvesting of oats, when compared show little relation to this ranking, nor are they even consistent with each other (Table 13).

We conclude from these data that during the three

TABLE 13. Comparison of Mowing and Harvesting Dates for the Winnebago Nest-Study Area in 1939, 1940, and 1941.

Date	Dates of first mowing of hay*	Ranking of seasons suggested by mowing dates	Dates of harvesting oats*	Ranking of seasons suggested by harvest dates
1939.....	June 12-July 5	Earliest (?)	July 11-22	Earliest
1940.....	June 15-June 29	Middle (?)	July 17-24	Latest
1941.....	June 17-July 9	Latest	July 15-23	Middle

*Exceptionally early and late dates in individual fields omitted.

years this investigation was carried out, no one growing season was sufficiently "earlier" than the others to cause all agricultural practices to be carried out earlier during that season than during the others.

The time of onset of nesting is certainly related to the duration of daily light periods (Bissonnette and Csech, 1941) and possibly also to age composition of the population and to such psychological stimuli as weather conditions, plant growth, and population densities. Once nesting is begun in earnest, re-nesting might be expected to obscure any basic patterns of seasonal progress. In lieu of extensive data from examination of pheasants' gonads, the only way to derive information on patterns in the progress of nesting seasons was to analyze trends of nest-establishment and hatching in relation to time. Such analysis is presented in Figures 14-18.

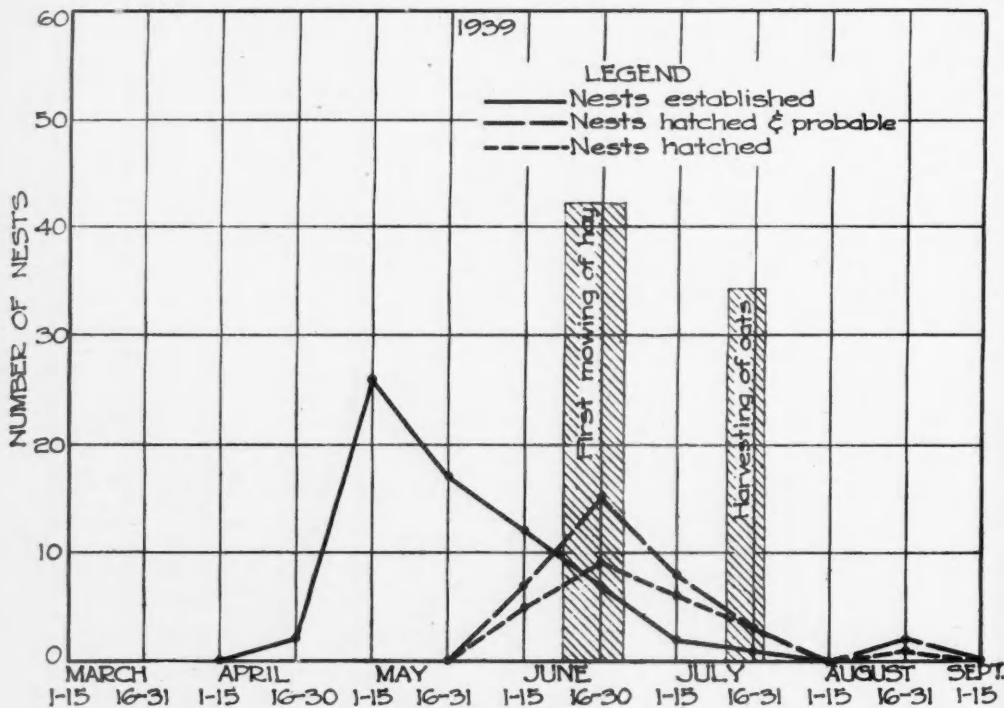


FIG. 14. Bi-monthly Trends of Nest Establishment and Nest Hatching, 1939.

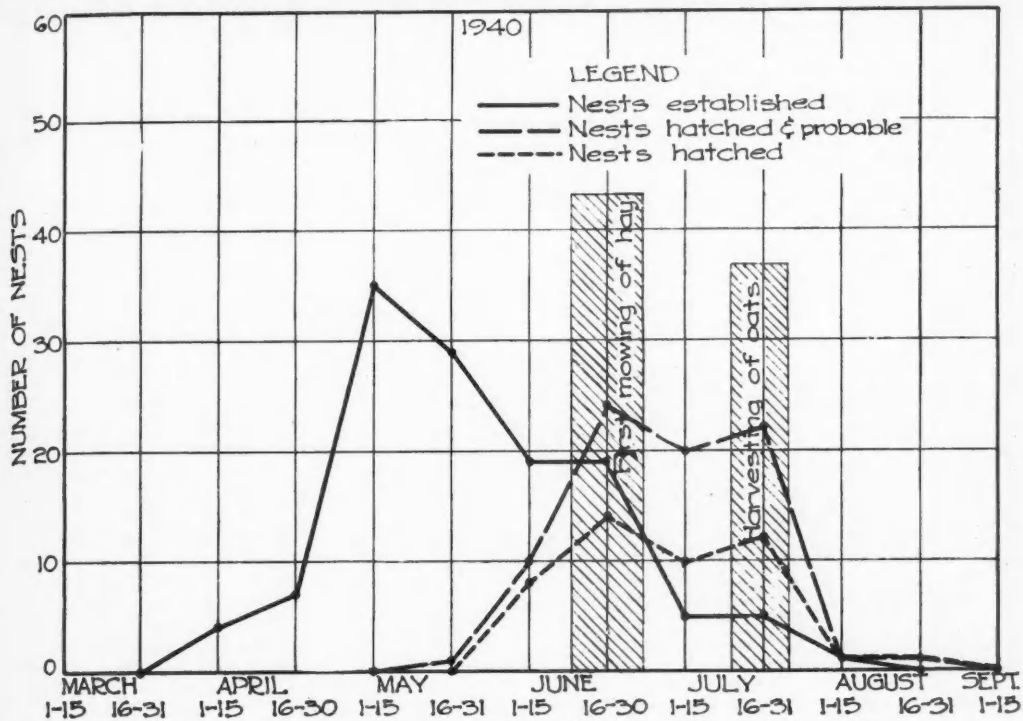


FIG. 15. Bi-monthly Trends of Nest Establishment and Nest Hatching, 1940.

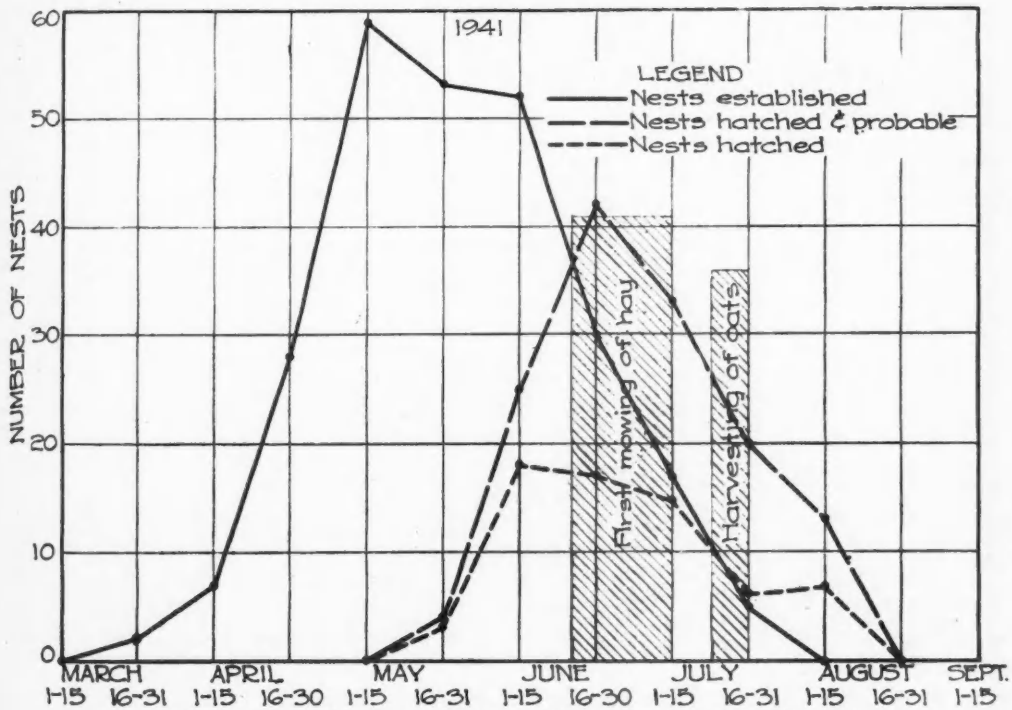


FIG. 16. Bi-monthly Trends of Nest Establishment and Nest Hatching, 1941.

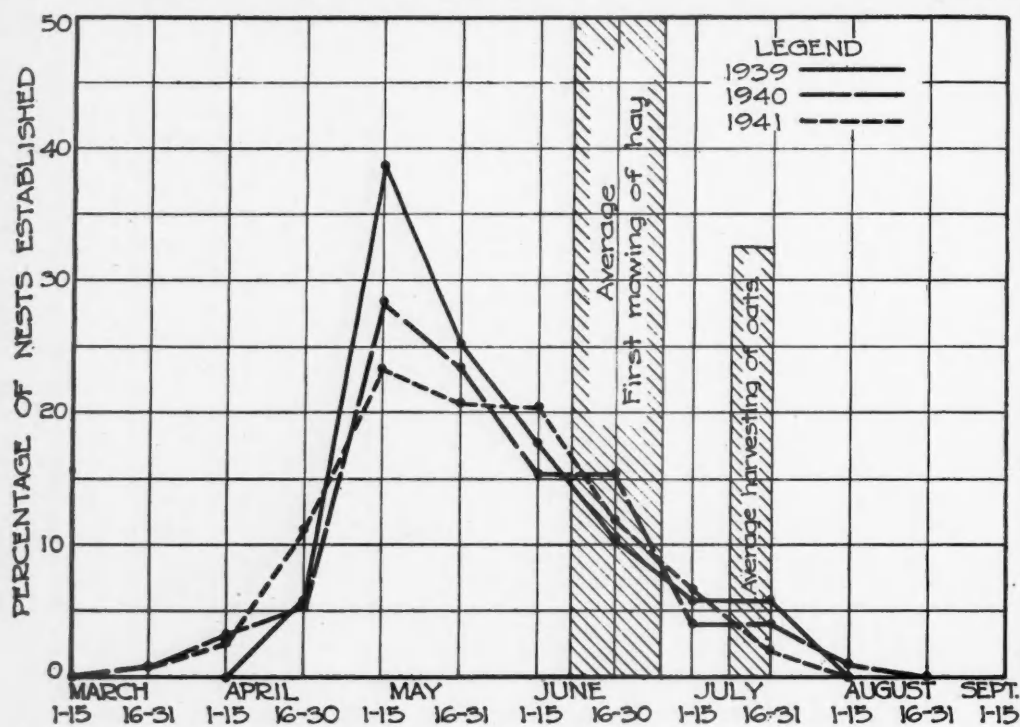


FIG. 17. Bi-monthly Percentages of Total Nests Established in 1939, 1940, and 1941.

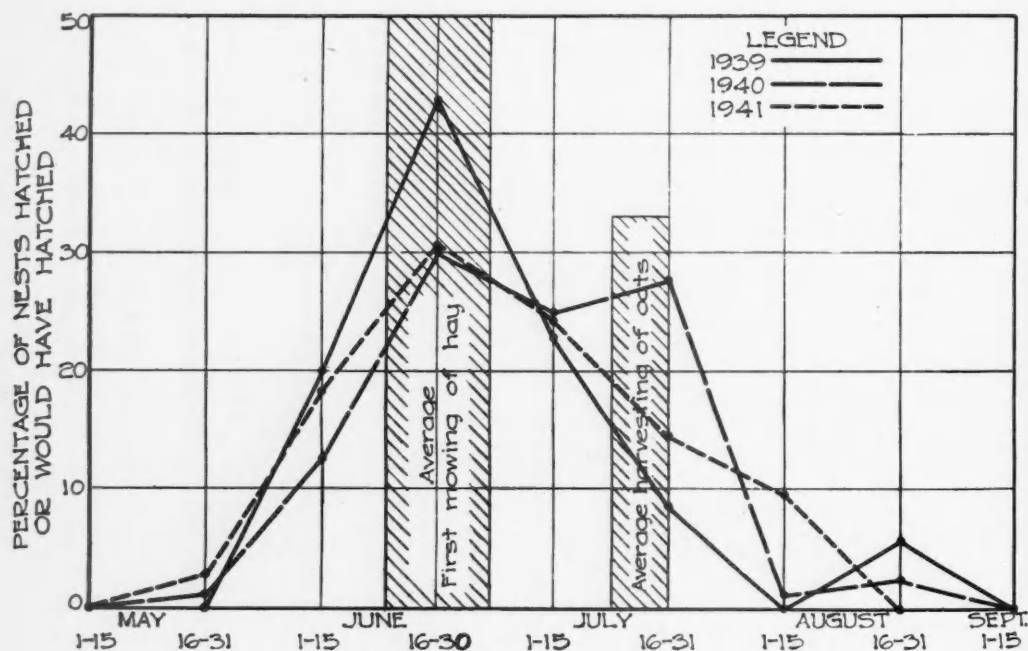


FIG. 18. Probable Hatching Trends for All Incubated Nests.

Although each nesting season progressed in its own peculiar fashion, nest-establishment began at about the same time each year, rapidly approached a peak, and in all three cases the peaks came within the same period of two weeks (Figure 17). The rates of establishment of nests for the three years were generally similar before the peaks were reached, except that nesting got off to a somewhat better start in 1941 than in the other years. However, following the peaks, the curves show differences. In 1939, the rate of establishment of nests fell rapidly after May 15, whereas, in the other two years, the rate tended to descend more slowly.

The net effect of the factors regulating time of onset of nesting may not have varied greatly from year to year. Consequently, nest-establishment proceeded in straightforward manner to a peak, beyond which the effects of other environmental factors appeared. Vagaries in the descents of the nest-establishment curves (Figure 17) may be traceable to re-nesting following the destruction of earlier nests by any agent whatsoever. In 1939, percentage of loss of nests was lowest, and in Figure 17, the 1939 curve falls more rapidly and uniformly than the others, perhaps indicating that lessened re-nesting in 1939 permitted nest-establishment to follow a basic pattern closely. This indication was strengthened through assignment of broods observed each year to the periods in which the nests producing them were begun. In 1939, 54 per cent of the broods seen came from nests begun May 1-15, and following that period the numbers dropped sharply. In 1940-41, one-third or fewer of the broods seen came from nests started May 1-15, and the numbers whose nests were established after that period were high. In 1941, percentage of loss was greatest, and the nest-establishment curve retreats slowly from its peak, indicating much re-nesting.

The curves showing bi-monthly trends of nest-hatching (Figures 14, 15, and 16) and those showing probable hatching trends for all incubated nests (Figure 18) reflect the general trends of the nest-establishment curves for the same year. Probable hatching trends include both actual hatching dates of successful nests and computed hatching dates of unsuccessful incubated nests.

These curves show clearly how mowing takes a heavy toll of nests and females each year, since it is performed during a period when the greatest proportion of nests are ready to hatch. However, gross annual differences in success of all hayfield nests cannot be divined by examination of the graphs. One might expect greater proportional losses from haying in 1940 than in 1941, for in 1940 mowing occurred before and during the time of maximum probable hatching, while in 1941, it came relatively later (Figures 15 and 16). Actually, the percentage of success in hayfields was nearly the same during the two years.

The fact that earlier nesting and later mowing in hayfields results in more successful nesting therein has been convincingly demonstrated by Randall

(1940) and Strode (1941). The analysis presented above does not discredit their findings but does show that at least during the three years in which the Winnebago studies were made, there was not enough variation in adjustment of nesting progress and mowing time to show correlative differences in hayfield success. It may be added that the last statement could also be applied to oats fields. The relation of nesting progress to timing of agricultural activities did not seem to be the key to the observed differences in yearly nesting successes during the Winnebago studies.

SIGNIFICANCE OF LOSSES

In terms of total production of pheasants the great losses of nests are not so important as they seem at first, for Errington and Hamerstrom (1937) have found that from 70 to 80 per cent of female pheasants re-nest until they bring off one successful brood. When analyzed according to Errington's (1942) method, the Winnebago data showed 73 per cent of the females nesting until they succeeded.

There are three possible advantages in having a high proportion of early nests successful: (1) early clutches average larger than late ones, (2) success of early nests lessens the probability of hens being killed by mowers, and (3) early nests might be expected to produce a more satisfactory type of bird for the bag than very late nests.

Females killed or badly injured by mowers or predators are rendered incapable of reproduction and the losses through mortality of females consequently assume an importance not suggested by comparison of their numbers with those of losses of nests from other causes.

Failure of some eggs to hatch in successful nests represents a source of absolute reproductive loss, but this failure is probably characteristic of the pheasant and largely unpreventable.

It is evident from examination of Table 14 that the rates of summer gain of the pheasants were not directly related to the percentages of nests succeeding. The plausible explanation for the high rate of gain in 1941, as based on increments of young at the seven-week stage, is greater re-nesting vigor, for in 1941 both percentage of success of nests and survival of juveniles were lowest. Even if differences in nesting losses could have been correlated with predation rates and timing of agricultural activities, it is questionable how real their effects would have been on production. Moreover, in view of the im-

TABLE 14. Comparison of Rates of Gain with Percentages of Success and Brood Size.

Year	Percentage of nest successful	Mean number chicks per brood at age of 7 weeks	Percentage increase of pheasants (from enumeration, 1939 and 1940, calculated 1941)
1939.....	36.0	6.1	180
1940.....	25.0	5.8	163
1941.....	23.2	5.3	220

portance attributed by Errington (1945) to density factors in relation to rates of gain and survival, one may well wonder how significant individual causes of nesting loss can be.

JUVENILE MORTALITY

Mortality of young pheasants after they leave the nests is a source of considerable reproductive loss, and can be measured on a loss-per-brood basis by counting the numbers of chicks in broods of different age classes. The relation of age to the size of broods for the three years is shown in Table 15.

TABLE 15. Relation of Age to Size of Broods.

Age of Young	Number of broods counted				Mean number of chicks per brood			
	1939	1940	1941	Total	1939	1940	1941	3-year means
1-3 weeks.....	3	1	7	11	8.3	2.0	5.1	5.7
4-5 weeks.....	15	16	21	52	7.3	6.5	5.2	6.2
6-7 weeks.....	28	29	24	81	6.1	5.8	5.3	5.7
8 weeks and more...	25	12	8	45	6.9	6.2	5.4	6.5

The general tendency is, of course, for broods to become smaller as the chicks become older. The mean numbers of chicks per brood in 1939 show this decrease consistently until the age-group, "eight weeks or over," is reached. The large number of chicks per brood in this category is undoubtedly due to the banding of broods, a source of error mentioned by Errington and Hamerstrom (1937). Chicks one to three weeks old rely upon concealment rather than flight to escape their enemies, and are, therefore, hard to see and count. Few counts of chicks in this age group were taken, and, even in some of these cases, it was questionable whether all chicks were seen. Chicks four to seven weeks old are relatively easy to flush and these counts seem reliable. Broods in the six to seven weeks group averaged larger than those in the four to five weeks group in 1941, possibly indicating that the pressure of very high pheasant population resulted in some banding of broods less than seven weeks old. Also, there is indication of heavy mortality to very young chicks in 1941, followed by a low rate of mortality at least until the observations were ceased in August.

Average losses of young per brood from time of hatching until the chicks were seven weeks old are as follows: 1939, 2.6 chicks; 1940, 3.3 chicks; and 1941, 3.3 chicks per brood.

Quantitative data for the causes of mortality among young pheasants were not obtained, but a few chicks were known to have been mashed by hens before leaving the nests, a few were run over by automobiles, and a few were killed by farm dogs. Several predatory animals which may have taken their tolls were resident on the area. Four to six marsh hawks hunted regularly over the 1,520-acre plot during the three years, and in 1941, one pair nested on the plot. Since these hawks were found to prey rather heavily on young pheasants in north-

west Iowa (Errington and Breenridge, 1936), some of the losses may be attributable to them.

Randall (1940a) was able to ascertain causes of about two-thirds of juvenile losses on a circumscribed area in Pennsylvania. He found that the most serious single factor in juvenile mortality was mowing, which was accountable for 18.8 per cent of the chicks killed.

PRODUCTION

The total production at the nest of pheasant chicks on the Winnebago nest research area during 1939, 1940, and 1941, could be derived simply from the nesting data at hand if the relation between numbers of nests found and total nests present were known. However, it was impossible to determine this ratio with great accuracy. In hayfields which had been patrolled not long before mowing, the observer's findings averaged less than half as many nests as checks after the mowing revealed. Examination of hayfields and small grain fields after mowing and harvesting resulted in the finding of a very high proportion of nests in these fields current at the time, thereby raising the ratio of nests found to total nests. Furthermore, the method of finding nests was somewhat selective for hatched nests, for they were usually recognizable for a period of about two or two and one-half months, unless plowed up. Assuming, in view of these facts, that some two-thirds of all hatched nests were found, we may calculate production.

In 1939, 27 nests were known to have hatched on the 1,520-acre plot, and 235 chicks were brought off from them. Multiplying this figure by three-halves to correct for nests not found, we have 352 chicks leaving the nests.

In 1940, 35 successful nests were found, and about 319 chicks were brought off. The number of chicks, 319, was derived by multiplying number of hatched nests, 35, by the average number of hatched eggs per successful nest, 9.1. The average number of hatched eggs per successful nest was calculated from only 32 nests, which supplied necessary data (see Table 10). Multiplying 319 by three-halves to correct for hatched nests not found, we find about 478 chicks leaving the nests in the 1,520-acre area.

In 1941, 74 nests were known to have hatched, and about 636 chicks were brought off from them. (This figure was derived according to the method used for the 1940 data.) Multiplying by three-halves to correct for hatched nests not found, we find that some 954 chicks left the nests on the 1,520-acre area in 1941.

In 1939, about 2.6 chicks per brood had been lost by the time the chicks were seven weeks old. Multiplying 2.6 by three-halves by 27 gives 105, the total estimated number of chicks lost during the first seven weeks of life. By subtraction, we find about 247 chicks having attained an age of seven weeks.

In 1940, 3.3 chicks per brood had been lost before reaching their seventh week, and the estimated total

loss for the area was 173. By subtraction, some 305 chicks attained the age of seven weeks.

In 1941, 3.3 chicks per brood suffered mortality before they were seven weeks old, and the estimated total loss was 366. By subtraction, about 588 chicks reached the age of seven weeks.

Correction of these figures to chicks per section (640 acres) gives the estimates as presented in Table 16.

TABLE 16. Estimated Number of Chicks Per Section Attaining the Age of Seven Weeks.

Year	Estimated number of chicks
1939.....	104
1940.....	128
1941.....	248

It has been pointed out that the mortality rate of chicks older than seven weeks was not known, but disregarding this fact for the moment, we may arrange a population schedule (Table 17) which is self-explanatory.

TABLE 17. Population Schedule for Winnebago Nest-Study Area, Pheasants Per Section.

Item	1939	1940	1941
Breeding population (based on enumerations).....	50	80	120 - 130
Estimated increment, round numbers.....	100	130	250
Estimated fall population.....	150	210	370 - 380
Fall population* (based on enumerations).....	130 - 150	200 - 220	no data

*Enumerations carried out over an area of about 688 acres in and adjacent to the nest-study area.

With allowances made for mortality to chicks older than seven weeks, fall population figures, based on estimated production, compare closely with those based on enumerations. (Methods of enumeration are discussed under "Techniques.") The validity of this analysis remains open to some question because of dangers of error through influx and egress, because of the assumption that two-thirds of hatched nests were found, and because of the familiar difficulties in enumerating pheasants. Despite these possible sources of error, it is felt that the census checks in 1939 and 1940 speak for themselves.

The Winnebago data were analyzed according to Errington's (1942) method, with the results shown in Table 18. According to this analysis 72.6 per cent of all females nested successfully, and the production figure was about six young to a hen (successful or not). Direct calculations based on the nesting and enumeration data give a figure of 4.5 chicks per hen for the three years. The truth may lie between these two figures.

TABLE 18. Productivity of a Sample of 100 Pheasant Females Calculated According to Errington's (1942) Method, Using Combined Winnebago Data for 1939, 1940, and 1941.

Period during which clutches were begun	Calculated number of females laying in initial and re-nesting attempts	Calculated number of clutches successful	Calculated number of hatched young
First Half			
April.....	6.0	1.0	16.0
Second Half			
April.....	49.7	7.6	77.5
First Half			
May.....	51.7	20.8	214.0
Second Half			
May.....	48.6	16.2	143.0
First Half			
June.....	17.1	4.4	33.6
Second Half			
June.....	16.0	6.8	49.0
First Half			
July.....	23.3	9.8	58.8
Second Half			
July.....	12.1	6.0	6.0
Total.....	224.5	72.6	597.9

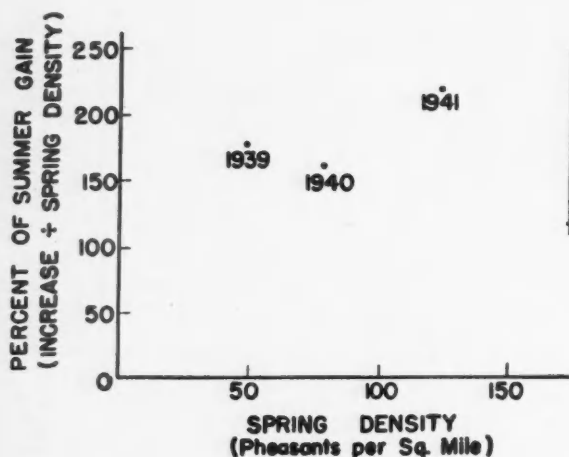
DENSITY EFFECTS

Data from the Winebago Area on rates of summer gain in relation to breeding density of pheasants, European partridges, and the two species combined are tabulated and plotted in Figure 19. The data for pheasants are reliable, the only weak point being the use of a production estimate in calculating a fall density figure for 1941, in lieu of enumeration data for that period. (See Table 15.) As stated previously, these production estimates gave fall population figures which closely agreed with data from enumerations in 1939 and 1940. The information on European partridges is of lower quality, but the general trends of reproductive gain in partridges are probably shown correctly, and the numbers of this species were not great enough to obscure the data for the much more plentiful pheasants.

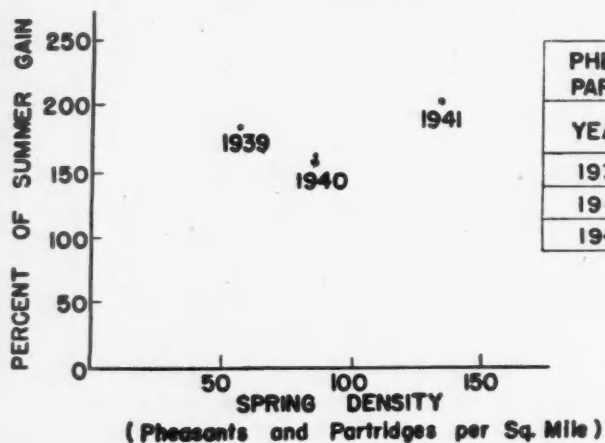
The graph for pheasants shows low breeding densities in 1939 accompanied by a rather high percentage of increase. In 1940, breeding densities were higher, but percentage of increase was lower, indicating inverse ratios of rates of gain to nesting densities as suggested by Errington (1934) in his earlier work with the bobwhite. The year 1941 brought still higher breeding densities accompanied by higher rates of gain, perhaps indicating what Errington (1945) has termed a more favorable reproductive phase.

Since partridges and pheasants occupy essentially the same ecological niche, and in view of Errington's (1945) finding evidences of competitive effects in population recovery studies of various Galliformes, it is reasonable to expect competitive influences of the two species to be present in this case. Such competition is in fact indicated by the data, with percentage of gain among the partridges decreasing as pheasant densities increased.

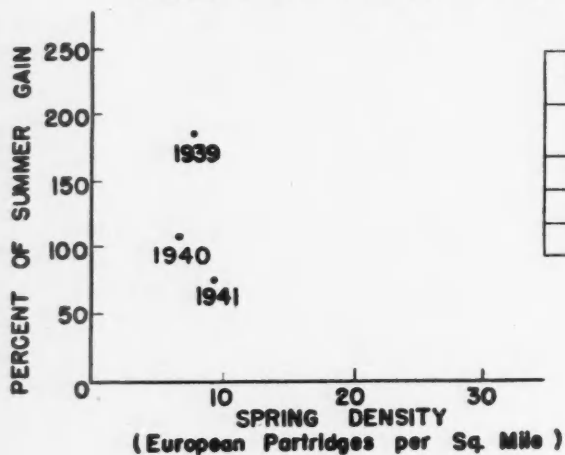
In Figure 20 are plotted data presented by Bach (1944) for pheasants in North Dakota. Of these data, Errington (1945, p. 25) wrote that they suggest depressed rates of summer gain for low May



PHEASANTS ONLY, WINNEBAGO AREA			
YEAR	SPRING DENSITY	FALL DENSITY	PERCENT OF SUMMER GAIN
1939	50	140	180
1940	80	210	163
1941	125	400	220



PHEASANTS AND EUROPEAN PARTRIDGES, WINNEBAGO AREA			
YEAR	SPRING DENSITY	FALL DENSITY	PERCENT OF SUMMER GAIN
1939	58	163	181
1940	86.4	223.3	158
1941	134.6	416.8	210



EUROPEAN PARTRIDGES ONLY WINNEBAGO AREA			
YEAR	SPRING DENSITY	FALL DENSITY	PERCENT OF SUMMER GAIN
1939	8	15	188
1940	6.4	13.2	106
1941	9.6	16.8	75

FIGURE 19

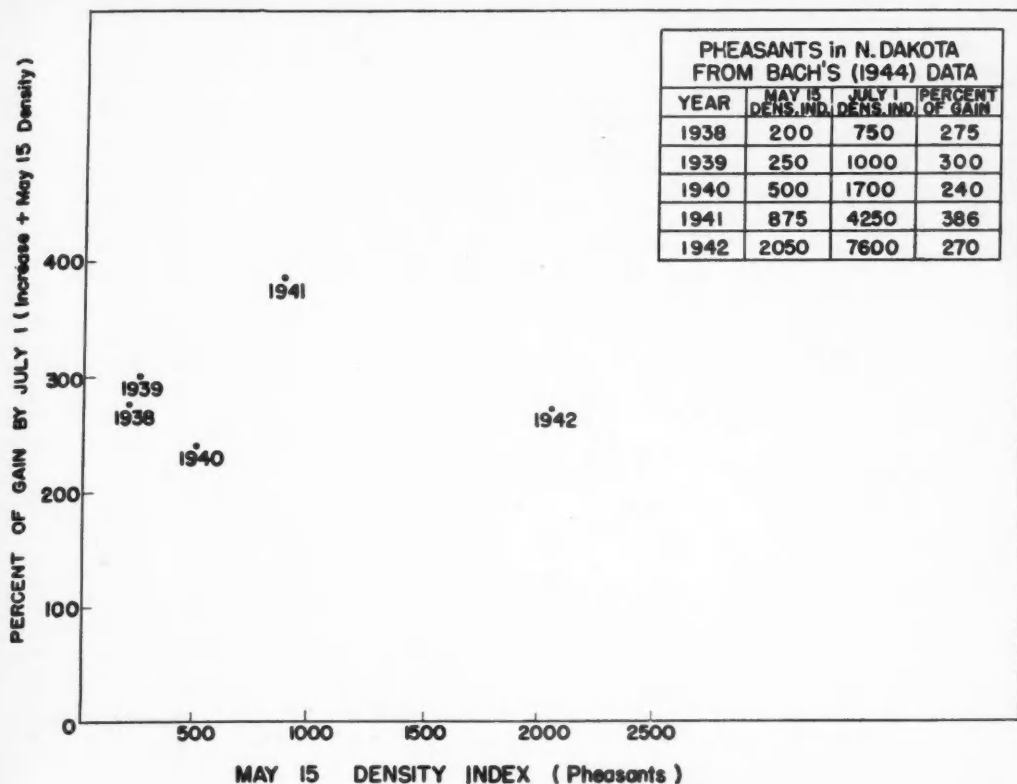


FIGURE 20

densities in 1938; gains in inverse ratio to somewhat higher densities in what may be interpreted as a more favorable phase, 1939-40; and gains in inverse ratio to still higher densities at a very favorable phase in 1941-43.

The Winnebago data are not strictly comparable to Bach's (1944) information, for the latter figures were placed on an index basis, unrelated to area, and the annual gains were computed from Bach's July 1 counts, when hatching is not yet complete.

Despite the differences mentioned, Bach's (1944) figures and the Winnebago data show the same general trends in relationship of gains to density for 1939-41, with fairly high rates of increase in both 1939 and 1940, those of 1940 tending to be inversely related to increased density, and very high rates of increase in 1941, with high breeding densities. In the case of the Winnebago data, I am not able to state whether these variations in rates of gain were functions of cyclic changes in capability to reproduce and survive superimposed upon density effects, or whether they were at least partially influenced by interplay of local environmental factors. At any rate, the similarities between the Winnebago and North Dakota information suggests the operation of mechanisms effective over a wide area rather than strong influence of local conditions on population

gains. Unfortunately, the North Dakota figures are the only published information on pheasant reproduction during this period from the north-central states available for comparison; other such data from this region are complicated by the presence of large numbers of Galliformes other than pheasants.

Einarsen's (1942) data for population trends of pheasants on Protection Island, Washington, indicated the same tendencies in 1939 and 1940 as did Bach's (1944) information and the Winnebago data: low densities and high rates of gain in 1939 followed by higher densities and lower rates of gain in 1940. For 1941, however, Einarsen's figures showed very high densities with still lower rates of increase, and failed to manifest the extremely favorable phase indicated for pheasants of the north-central states in that year.

SUMMARY

(1) An investigation of nesting and natural production of the ring-necked pheasant (*Phasianus colchicus torquatus* Gmelin) was made in north-central Iowa during the breeding seasons of 1939, 1940, and 1941.

(2) Studies were carried out on a 1,520-acre portion of the Winnebago Research Area in Winnebago

County, Iowa. Lying within the Wisconsin drift area, the 1,520-acre plot is level or moderately sloped, except for two relatively high ridges. About 90 per cent of the land was in direct agricultural use as crop, hay, or pasture land.

(3) Winter habits of the pheasant are described, and their redistribution and changes in behavior with the advent of spring are discussed.

(4) The places at which crowing occurred are described in detail, and it is concluded that the presence of objects such as stones, etc. were not required. Any location which permitted the males to be locally conspicuous seemed satisfactory for crowing. Returning to an exact spot used before for crowing was infrequent and probably accidental.

(5) The localization of each male within a region of the available range through April until mid-May, at least, and probably throughout the breeding season, was a phenomenon of general occurrence.

(6) There was probably a tendency toward the establishment of crowing areas or territories by the male pheasants, but these territories were thought to be very plastic and subject to frequent readjustments.

(7) Fighting among males, though often precipitated by the presence of females, appeared usually to be caused by attempted intrusions among males. In a few instances, fighting may have been over females.

(8) The choice of nesting sites probably rested with hens, and the males possibly adapted their territories to include nests.

(9) Lack of suitable cover for crowing areas could scarcely have limited pheasant reproduction on the Winnebago Area, but territorial competition of an indirect sort influenced by density may have had a limiting effect.

(10) The knowledge of territoriality among pheasants under conditions of high densities, large fields, and few natural boundaries could probably be greatly furthered by an intensive study of this phase alone if great numbers of birds were marked.

(11) The male/female ratios were estimated to be as follows: 1:2.4 in 1939, 1:2.1 in 1940, and 1:2.0 in 1941.

(12) The earliest nest found was begun in the two-week period, March 16-31, 1941. The latest nest observed was established during the first half of August, 1940.

(13) New eggs generally appeared in nests at a rate slightly lower than one per day, but exceptions were noted when more than one female contributed to a clutch.

(14) While the females were incubating, they were rarely found away from the nests. No regular "rest periods" were noted.

(15) The degree of disturbance to incubating females by the observer was capable of regulation through the manner of approaching the nests.

(16) During the three years location data were obtained for 533 pheasant nests, and other data were obtained for varying numbers of these nests. Nests

were found by repeated systematic patrolling of fields, and by checking in all hayfields and small grain fields as soon after removal of cover as possible.

(17) Nests were found in a variety of cover types, but hayfields, fields of small grain, and fence rows consistently harbored the largest numbers. Hayfields contained from 34.6 to 64.8 per cent of all nests; small grains, from 19.5 to 22.9 per cent; and fence rows held from 6.6 to 25.3 per cent of the nests. As nesting densities increased, the proportions of hayfield nests increased.

(18) The proportion of nests successful in small grain was high (40.3-80.0 per cent); in fence rows, low (4.8-21.1 per cent); and in hayfields, intermediate (20.3-34.6 per cent).

(19) Nests in types of hay mowed late had higher percentages of success than those in types of hay mowed early. For example, mowing of native hay generally followed the first mowing of alfalfa by 10 to 14 days, and a higher proportion of nests was usually successful in native hay than in alfalfa.

(20) Percentages of success for all nests found during the three years were as follows: 1939, 36.0 per cent; 1940, 25.0 per cent; and 1941, 23.2 per cent.

(21) Losses of nests were attributed to many causes, of which desertion, predation, injury to female, and death of female were the important types. Over a third of all nests lost were deserted as a result of disturbance by man in pursuing agricultural activities. Crows were the most destructive predators, probably having caused losses of 19.0 per cent of all destroyed nests. Haying, together with subsequent desertion and predation, accounted for 35 per cent of nesting failures.

(22) Attempts to correlate meteorological data, dates of first field work, dates of mowing, of hay, and dates of harvesting small grain for the three years showed that no one growing season was sufficiently advanced to cause the carrying out of all these agricultural practices consistently earlier during one year than during another.

(23) It appeared that there is a basic rhythm of nest-establishment which results in direct procedure of rate of establishment to a peak; beyond the peak the basic rhythm is obscured by renesting.

(24) The relation of nesting progress to timing of agricultural activities did not seem to be the key to observed differences in yearly nesting successes during the Winnebago studies.

(25) The significance of nesting losses is discussed, and it is concluded that failure of individual nests does not necessarily signify absolute reproductive loss, for, as pointed out by other workers, many hens renest until they bring off a brood.

(26) It is shown that rates of summer gain of the pheasants were not directly related to percentages of nests succeeding nor to differences in juvenile survival. Yearly differences in rates of gain seemed accountable to success of early nesting or to differences in renesting vigor, at least when these rates

of gain were based on increments of young at the seven-week stage.

(27) It was estimated that in 1939, 352 chicks hatched and left the nests on the 1,520-acre study area; for 1940, the estimate was 478, and for 1941, 954.

(28) During the first seven weeks after hatching, there were losses of about 2.6 chicks per brood in 1939, 3.3 chicks per brood in 1940, and 3.3 chicks per brood in 1941. The following estimated number of chicks attained the age of seven weeks: in 1939, 247; in 1940, 305; and in 1941, 588.

(29) Estimates of production derived from nesting data agree rather closely with enumeration data taken before and after the nesting seasons, but attention is called to the assumptions made in the derivation of the estimates and to the difficulties in enumerating pheasants. Enumeration was accomplished in the spring by repeated total counts over the nest-research area and in the fall by flushing counts during the hunting season and by roadside counts.

(30) Data on rates of summer gain in relation to breeding densities of pheasants, European partridges, and the two species combined are plotted. Some evidences of competitive effects between the two species are evident; the combined data show trends of gain in relation to density similar to those shown by data for pheasants in North Dakota during the same years.

(31) It is not known whether the observed variations in rates of gain were functions of cyclic changes in capability to reproduce and survive superimposed upon density effects, or whether they were at least partially influenced by interplay of local environmental factors.

(32) Synchronism between the Winnebago and North Dakota population phenomena suggest the operation of mechanisms effective over a large area rather than strong influence of local conditions on population gains.

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ECOLOGY OF THE SPONGES OF A BRACKISH
WATER ENVIRONMENT, AT BEAUFORT, N. C.

M. W. DE LAUBENFELS

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ECOLOGY OF THE SPONGES OF A BRACKISH WATER ENVIRONMENT, AT BEAUFORT, N. C.

INTRODUCTORY REMARKS

Beaufort is on the central coast of North Carolina. Opposite the city and harbor occurs a two-kilometer gap in the nearly continuous long narrow islands called "banks" which lie off-shore for so much of the mid-Atlantic coasts. Inside these banks are areas of hundreds of square miles of shallow lagoons called "sounds." Newport River, North River, and a number of smaller streams empty fresh water into the lagoons in the vicinity of Beaufort, accounting for the break in the banks, and (with its help) accounting for the natural harbor. Man has deepened and altered this to his own ends.

The area that is here considered is part of the AQUATIC REALM or water environment, and its subdivision the LITTORAL PROVINCE. Before human

interference, nearly all of the Beaufort region belonged to the subdivision of the Littoral Province known as SHIFTING BEACH FORMATION, and much of it still belongs there. Sponges occur very seldom on sand, mud, or other shifting substrata, but throughout the ages, some substantial foundations for sponges have been provided by shells of living and of dead animals. In recent years, mankind has provided additional good places for sponge attachment by building wharves, bridge foundations, breakwaters and various types of walls within the water. Sponges occur abundantly on such substrata, or HARD BEACH FORMATION.

Near Beaufort, and opposite the above-mentioned gap in the line of outer banks, lies a small island, not quite a kilometer long, called Piver's Island.

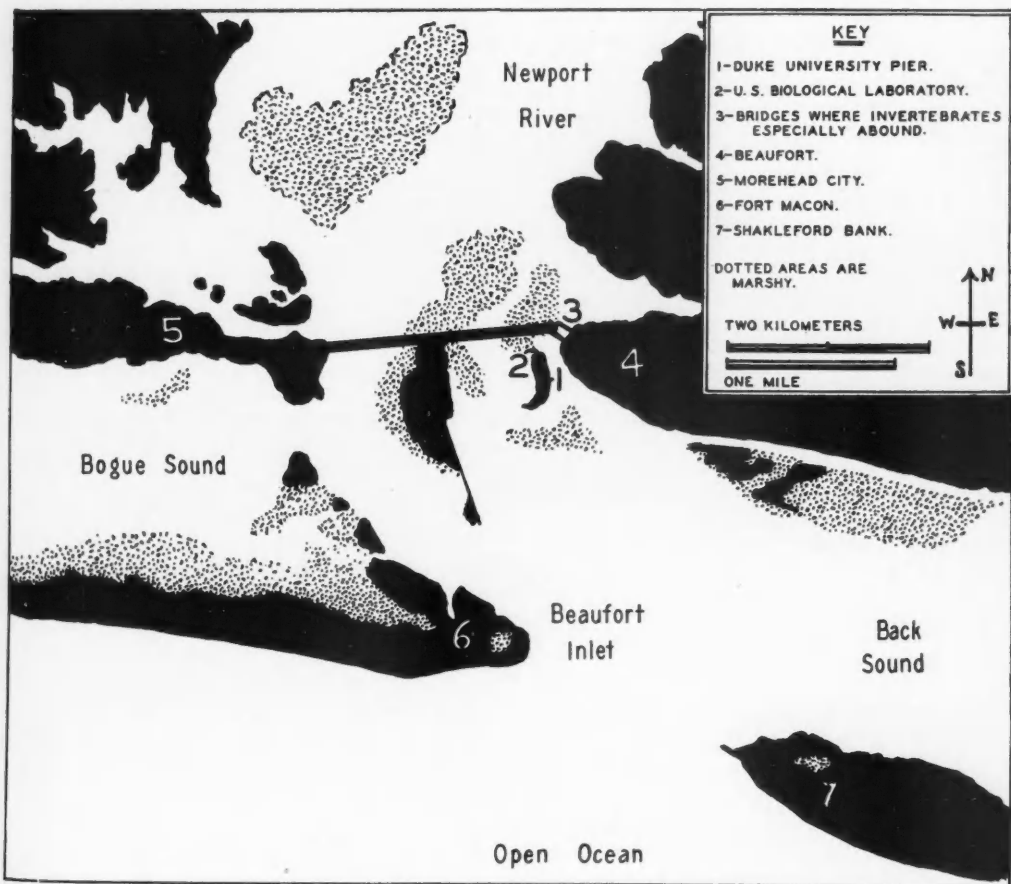


FIG. 1. Map of Entrance to Beaufort Harbor.

On its south end, toward the open ocean, are the laboratories of the Marine Station of Duke University, and at its north end is the U. S. Fisheries Biological Laboratory. The observations here embodied have been made possible only by the generosity of these two institutions, and appreciation is here expressed to both of them. Appreciation is also due for help rendered by Dr. A. S. Pearse of Duke University, and Dr. H. F. Prytherch, resident director of the Fisheries Laboratory.

In the following discussion, the environment is analyzed as physical, chemical, and biological. The physical and chemical as here designated refer to those environmental effects that do not immediately arise from living organisms; all that do so arise are expressed in physical and chemical means, but are here given their own special category, that is to say: biological.

This discussion is intended as an introduction or stimulus, rather than the last word on the subject. It is based upon personal study only during the summer of 1946, obviously too brief a time for final report. Some pertinent matters have been studied over longer periods of time by other investigators, and the reports of their findings have been drawn upon liberally. Continuing study may be expected to occur at the Fisheries Laboratory and at the Duke University Marine Station; it is hoped that some of this study may advance this ecological study, adding statistical data, new observations, and more complete conclusions.

PORIFERA OF BEAUFORT

There are at least fifteen kinds of sponges in the vicinity of Beaufort. The foundation for their study has been Fisheries Document No. 876, by George & Wilson, published in 1919. Unfortunately the names that are used in it warrant considerable amending, therefore a discussion is here interposed, to correlate its designations with those that should be employed.

The author would like to emphasize that his own first paper on sponges needs revision as urgently as does this first paper on sponges by Dr. George. Twenty years of intensive study of sponges in the field in many parts of the world has had a considerable effect. Study of the type specimens in European museums has helped even more toward an understanding of sponge relationships, because most of these basic types were established more than fifty years ago, and because prior to the work of H. V. Wilson, descriptions of Porifera were very badly done, so that the specimens must be seen. The descriptions in Fisheries Document No. 876 are superlatively good.

ANNOTATED LIST OF SPECIES

1. *Spirastrella andrewsii*, called new. The author studied not only the description in the bulletin, but also the original specimens in the U. S. National Museum. They are all obviously of the extremely distinctive and super-abundant West Indian species

which the sponge fisherman call "loggerhead"; the largest sponge specimens that are known, are of this species. It was first described as *Alcyonium vesparium* by Lamarek in 1815. Later authors put it in *Spongia*, in *Suberites*, in *Hardwickia*, in *Thalysias*, in *Hymeniacidon*, in *Papillina*, and this paper adds *Spirastrella* and *Poterion*. It is clearly not congeneric with the proper members of any of these nine genera; instead it belongs in (and was made the type of) the genus *Sphecospongia* by Marshall. There is in the Fisheries Laboratory at Beaufort, a locally collected specimen (without date) of *Sphecospongia*. This was over 60 cm. in diameter when collected, and is very typical in all respects of the West Indian "loggerheads."

2. *Cliona celata* Grant. This is correctly identified.

3. *Poterion atlantica*, called new. This is also obviously the unique and strongly marked species *Sphecospongia vesparia*, exactly like number one.

4. *Suberites undulatus*. The characters of this sponge are so puzzling that the author was exceedingly anxious to find living specimens. Very careful search during the summer of 1946 failed to reveal any, and therefore this remains somewhat of a mystery. The 1946 search did yield specimens of sponge with exactly the very peculiar labyrinthoid structure of *undulatus*, but they proved to be *Microciona prolifera*, quite typical in nearly every respect. One must consider that dead specimens of *Microciona* change to the color which was described as being that of *undulatus*. Dead specimens of *Microciona* may lose the flesh spicules, and thus come to a residual spiculation very much like that of *undulatus*. No final identification of *undulatus* as being really conspecific with *Microciona prolifera* is as yet justified, but *undulatus* is so very different in habitus and ectosome from *Suberites* that it should be taken from that genus, and it should be listed as "incertae sedis."

5. *Tetilla laminaris*, called new. Because this has microsceres, it is definitely a *Craniella*, not a *Tetilla*. The only character to separate it from *Craniella crania* Mueller is that the Beaufort specimens were flattened on two sides, and many *crania* specimens are more nearly round. The difference is slight, and so likely to be due to ecological effects that there is no justification in calling this new. This is all the more noteworthy, in that *crania* is already known to be common on the east coast of the United States, as Verrill and others have pointed out. A damaged, and therefore dubious specimen of this was collected at Beaufort, offshore, in the ocean, in 1946.

6. *Reniera tubifera*, called new. This species was studied very carefully in 1946 at Beaufort and the author has also studied the cosmopolitan species *Haliciona permollis* Bowerbank in various parts of the world. The agreement extends to the most minute details; the Beaufort sponge is the very abundant cosmopolitan one.

7. *Stylotella heliophila* Wilson. This is clearly a typical *Hymeniacidon* and was first described by Parker in 1910 page 766.

8. *Esperiopsis obliqua*, called new. The description is definitely of the genus *Tenaciella*, but this does not settle the matter. Three of George & Wilson's specimens were collected on Fort Macon Beach in 1946. The author found in just that locality a specimen with the peculiar oblique chelas that gave rise to the name *obliqua*; this and the color and the principal spiculation all led to the natural assumption that *obliqua* had been found again. It happened, however, that a spicule study was made from another portion of the same specimen, and here the chelas and other spicules proved to be those of *Microciona prolifera*. Clearly the latter species in certain localities, notably Fort Macon Beach, suffers such changes to part or all of a specimen as to acquire the characters of *obliqua*. Such a sponge is still *M. prolifera*.

9. *Lissodendoryx carolinensis* Wilson. Comparison of descriptions shows no difference between this and the common West Indian sponge described as *Haliclona isodictyalis* by Carter and made the type of *Lissodendoryx* by Topsent. The author is familiar with the Beaufort sponge, and with *isodictyalis* as it occurs in the field, and emphatically confirms their conspecificity.

10. *Phloeodictyon nodosum*, called new. In the West Indies there occurs a very common sponge named *Rhizochalina oleracea* by Schmidt. The tenth Beaufort species is first of all a *Rhizochalina*. It differs a little from Schmidt's description of *oleracea*; he mentioned megascleres 2 by 85 to 3 by 143 microns, whereas *nodosum* is described as having megascleres 4 by 100 to 5 by 100 microns. The author has studied many West Indian specimens of *oleracea*, and finds that often the spicules range from 2 by 70 to 6 by 150 microns. The Beaufort sponge emphatically falls within the range of variation of clear-cut *oleracea*.

11. *Phoriospongia osburnensis*, called new. This sponge agrees in minute detail with the one which Dendy in 1896 described as *Desmacidon australis*; this same author in 1916 quite properly transferred this Australian species to the genus *Desmapsamma*.

12. *Microciona prolifera* Verrill. This famous species was first described, as Verrill observed, by Ellis & Solander.

13. *Axinella acanthifera*, called new. This is clearly a *Raspailia*, as H. V. Wilson pointed out in 1922, unless it might perchance turn out to be merely just another variant of the very versatile sponge, *Microciona prolifera*. The author has found many specimens of the latter in which the smaller spicules were extremely rare, and in large portions of some colonies of *M. prolifera* the smaller spicules are completely absent. Many specimens of clear-cut *Microciona* have exactly the external shape of *acanthifera*; were they also to lack the smaller spicules they would conform to the description of *acanthifera*. The color is the same. *Acanthifera* was based upon but a single specimen and must be regarded as a very dubious species; even the genus is uncertain.

14. *Acanthella corrugata*, called new. The comments made above need to be repeated here. This species is based upon a single damaged specimen found cast up on the beach. It may not be merely another form of *M. prolifera*, but the possibility exists that such is the case. It, too, is a very dubious species.

15. *Aplysilla longispina*, called new. This species was originally based on but a single specimen. It was studied again by the author in the summer of 1946, when it proved to be fairly common at Beaufort. The only difference that its original authors found between it and *A. sulfurea* Schmidt was slightly higher conules. There was agreement in all the many other very peculiar characteristics, such as bright yellow color in life, turning to dark blue or violet when dying. The 1946 study confirms the synonymy; this is *Aplysilla sulfurea*.

16. *Pleraplysilla latens*, called new. This is a good species.

17. *Hircinia ectofibrosa*, called new. Its authors compare it significantly to *H. variabilis* Schmidt. Study in 1946 of freshly collected specimens, together with the author's familiarity with *variabilis* as it occurs in other parts of the world, confirms the diagnosis; the Beaufort sponge is *variabilis*.

SUMMARY

1. *Spirastrella andrewsii*, new = *Sphēciospongia vesparia* (Lamarek) Marshall
2. *Cliona celata* Grant = *Cliona celata* Grant
3. *Poterion atlantica*, new = *Sphēciospongia vesparia* (Lamarek) Marshall
4. *Suberites undulatus*, new = genus et species incertae sedis
5. *Tetilla laminaris*, new = *Craniella crania* (Mueller) Schmidt
6. *Reniera tubifera*, new = *Haliclona permollis* (Bowerbank) de Laubenfels
7. *Stylotella heliophila* Wilson = *Hymeniacidon heliophila* (Parker) de Laubenfels
8. *Esperiopsis obliqua*, new = *Microciona prolifera* (Ellis & Solander) Verrill
9. *Lissodendoryx carolinensis* Wilson = *Lissodendoryx isodictyalis* (Carter) Topsent
10. *Phloeodictyon nodosum*, new = *Rhizochalina oleracea* Schmidt
11. *Phoriospongia osburnensis*, new = *Desmapsamma australis* Dendy.
12. *Microciona prolifera* Verrill = *Microciona prolifera* (Ellis & Solander) Verrill
13. *Axinella acanthifera*, new = genus et species incertae sedis
14. *Acanthella corrugata*, new = genus et species incertae sedis
15. *Aplysilla longispina*, new = *Aplysilla sulfurea* Schmidt
16. *Pleraplysilla latens*, new = *Pleraplysilla latens* George & Wilson
17. *Hircinia ectofibrosa*, new = *Hircinia variabilis* (Schmidt) Schulze

During the summer of 1946 (August 24) some sponges were collected at about 5 meters depth, half a kilometer off-shore in the ocean. One is a *Haliclona*, here dubiously identified as the species originally called *Pachychalina excelsa* by Schmidt, from northwestern Europe. This has never been well described; with a more complete knowledge it may prove to be not conspecific. The same must be said of *Pachychalina millepora* of Verrill, a Bermuda species. The surmise is here made, however, that *millepora* and the Beaufort specimen are conspecific with *excelsa*.

Together with *Haliclona excelsa*, specimens were collected of *Hircinia variabilis*, *Microciona prolifera* in its most extremely proliferated form, *Cliona celata* in large yellow masses, no longer boring, *Craniella crania* in very poor condition, and *Higginsia coralloides*. The condition of the latter may serve to call attention to the difficulties involved in sponge identification.

There were collected three specimens of *Higginsia*, but the three are so much alike that it is very possible that they are merely three fragments of a single colony, broken by or in the dredge. The largest piece was first studied, and it revealed a spiculation of only oxeas, with so few styles that they were considered accidental; in species of only oxeas an occasional spicule is often left as a style by malformation. Sample after sample was boiled out with nitric acid, but not a trace of a microscleere could be found. Therefore a provisional identification of the genus *Colloclaypta* was made. Then study of the two smaller specimens revealed a few of the peculiar acanthose microscleeres that characterize *Higginsia coralloides*, which is a common West Indian species. Here is a close parallel to the situation within a sponge mass that led George & Wilson to identify an abnormal bit of *Microciona* as being an *Esperiopsis*. Sponge identifications that are based on single specimens, or even on a few specimens, are always liable to subsequent revision if and when additional material is found.

CALYX POA, New Species

A sponge was found at Beaufort on July 26, 1946, which appears to be a new species and is here designated as *Calyx poa*. There is little likelihood that it will ever be synonymized with any other species of the genus *Calyx*, but it is possible that it is the ecological modification of some other genus. Painstaking study failed to bring forth any such evidence in 1946, but if the species keeps on growing at Beaufort it may display additional growth forms; these should be anticipated and sought.

The ecological placement of *Calyx poa* is noteworthy. Just west of the north end of the causeway that connects Piver's Island to the mainland there is an artificial enclosure called the "mullet pond." The tide rushes into this, then empties out at low tide, through two wooden-lined gates or sluiceways. The western of the two sluices was thickly coated with sponges, 10 to 15 cm. thick on the wood and on

adjacent concrete. The bulk of the sponges were bright orange Hymeniacidons, with a sprinkling of bright red Microcionas. Closer observation revealed a duller interstitial mass of sponges of the genus *Lissodendoryx*, bluish gray in color, and violet *Haliclona permollis*, nestling down in the cracks between the more prominent sponges. An occasion arose for the collection of large quantities of specimens of Hymeniacidon and only thus occurred the discovery of the masses of *Calyx poa*, which were regularly overlaid by the orange colored species. No trace of *C. poa* could be found other than close to the Hymeniacidon, nor anywhere except at the sluice gate. At that place a bucketful could have been collected by assiduous search.

The holotype of *Calyx poa* has been deposited in the United States National Museum (Number 22724). It, and the other specimens, are all amorphous masses of indefinite size; for convenience most were collected in the form of small handfuls. The surface, and thus the general appearance, is quite peculiar among sponges. One often sees a field of grain blown by the wind so that somewhat symmetrical waves are formed by the stalks—in one place all bent and in another place not bent. *Calyx poa* gives this some effect. That which corresponds to the stalks of grain is a dense pile of strands about 50 microns in diameter, and at least 3 or 4 mm. high above the surface of the sponge. These strands are the apical branchings of the skeletal fibers or traets which ramify throughout the main body of the sponge. There is no sharply marked surface, however, inasmuch as the surface pile blends into the endosome. The crests of the "wind swept" rows are about 5 mm. apart. If pressure of overlying sponges bent some of the pile down, why not all? As well as could be determined in the field, the shape of the surface of *Calyx poa* was completely independent of the greater or lesser extent to which it was or was not closely overlain by Hymeniacidon. The collector at once thought of this as the "wind-row sponge" and could readily detect the species by the very uniform and distinctive surface.

The color of living *Calyx poa* is chiefly a drab, with here and there hints of orange akin to that of Hymeniacidon and elsewhere hints of green. The latter probably indicates symbiont plant cells, the former may actually represent contributions of material from the over-lying species. When dry the sponge is pale gray. Alive, the consistency is like wet paper—dry it is like dry, pulpy paper. No oscules could be made out, but obviously the surface is porous at the bases of the surface strands, pores in the dry specimen 40 microns in diameter, 80 or more microns apart. These strands are not as free to move with respect to each other as are the stalks of grass in a pasture, but are somewhat interconnected in life by soft colloidal material. In the dry sponge this glues them together into brittle masses.

The endosome is cavernous, thickly penetrated by shaggy traets, which are a little larger, and not quite so abundant as the surface strands, because some of

these tracts separate at the surface into two or more divisions. There are ten to thirty spicules per cross-section of these endosomal tracts, not parallel, but in a rather shaggy disorder. They are held together by a sort of jelly rather than by obvious spongin.

The spicules are only oxeas, usually about 7 by 280 microns. Many are as large as 8 by 305 or as small as 6 by 255 microns. A few, probably juvenile, are only 1 by 90 microns.

The type of the genus *Calyx* is *nicæensis*, a common Mediterranean sponge. It is characterized by the spicular tracts that run all the way through the sponge without uniting to make a network as they do in most sponges. These tracts are furthermore exceptionally shaggy, the spicules in them not held neatly in parallel lines. The Beaufort sponge under discussion has both these traits, so that it may be regarded as congeneric with *nicæensis*. The Mediterranean sponge, however, is very dark in color, regularly assumes a cup or vase-like shape (hence the generic name) and its spicules are only about 6 by 150 microns in size. It certainly has some spongin in its tracts; *poa* may have a little, but is not obviously so provided.

Other species of *Calyx* include the following: *C. vaculum*, has strongyles in the spiculation but is otherwise very much like *nicæensis*, with which it may likely be conspecific. *C. stipitatus* and *C. clavata* are each club shaped, and perhaps conspecific with each other. There is so much difference between their spicules and those of the genotype that they perhaps should be taken out of *Calyx* and put in *Vagocia*. If the Beaufort sponge really belongs in *Calyx* it may be the second species of that genus. It is quite conceivable however, that eventually a new genus will need to be erected for *C. poa*.

Additional species of sponge may be found at Beaufort in the future. For the present we have listed fifteen kinds to consider.

SUMMARY OF SPECIES

A summary of the Beaufort sponges shows that of the fifteen, six are typical of the West Indies: *Spheciospongia vesparia*, *Lissodendoryx isodictyalis*, *Rhizochalina oleracea*, *Aplysilla sulfurea*, *Ircinia variabilis* and *Higginsia coralloides*. Four others are common also in the West Indies, but furthermore so widely distributed as to be termed cosmopolitan; *Cliona celata*, *Craniella crania*, *Haliclona permollis*, and *Haliclona excelsa*. Thus three fourths of the Beaufort fauna are West Indian. Only two Beaufort species are peculiar to the locality: *Pleraplysilla latens* and *Calyx poa*.

Five of the Beaufort sponges were found only in the open ocean, and are therefore essentially outside the territory that is here under discussion; they are *Spheciospongia vesparia*, *Rhizochalina oleracea*, *Ircinia variabilis*, *Haliclona excelsa* and *Higginsia coralloides*.

Of the ten species found inside the Beaufort Harbor region, several are not at all conspicuous and probably are not very significant ecologically there.

Craniella crania in 1946 was found only in the open ocean off-shore. Only a single specimen of *Rhizochalina oleracea* was ever found inside the harbor. *Pleraplysilla latens* could not be found at all in 1946. *Aplysilla sulfurea* and *Calyx poa* each were confined to a very limited and small area.

The remaining five species are very abundant and are certainly ecologically significant in Beaufort Harbor; they are *Cliona celata*, *Haliclona permollis*, *Hymeniacidon heliophila*, *Lissodendoryx isodictyalis* and *Microciona prolifera*.

The field collector or student may identify them thus:

MICROCIONA or "Oyster sponge"—bright red.

HYMENIACIDON or "Sun sponge"—bright orange.

CLIONA or "Boring sponge"—bright yellow.

LISSODENDORYX or "Garlie sponge"—dull greenish or blue, odoriferous.

HALICLONA or "Volcano sponge"—violet to gray, always with prominent oscules, like craters.

For precise identification, a bit of the sponge about the size of the head of a pin may be put on a glass slide with a few drops of ordinary laundry bleach (basically sodium hypochlorite solution, NaOCl). After a few minutes one teases it with needles to eliminate the bulk of the bubbles that result, puts on a cover slip and studies the spicules with the high power.

No account of the sponges that do occur at Beaufort can reveal the whole story. It is also very significant to observe the lack, to note the sponge faunas of other areas of similar size in comparison. The author, from his personal experience, can compare that area which at Beaufort (near Piver's Island) yields 5 species:

Puget Sound (Friday Harbor)	about 20
Panama (Balboa, Pacific side)	about 20
Coast of England (Plymouth)	about 30
Central California (Monterey)	about 30
Southern California (Laguna)	about 30
Mediterranean (Naples)	about 40
West Indies (Dry Tortugas)	about 60

The latter area is possibly the best in the whole world for sponges, but the fact remains that nearly any marine area, hard beach formation, will have several times as many species as is true near Beaufort.

Collecting by rowboat or wading near Piver's Island reveals large numbers of sponges, but one does not find more at extra low tides or by dredging. One need only look under water on a clear calm day, or by a "waterglass," to confirm the fact that below low tide mark the sponges stop abruptly, almost to zero. Here is the amazing thing, because in other parts of the world the reverse is the situation. Sponges usually are much more abundant below low tide.

When the strictly intertidal sponges of the world are studied, this distribution at Beaufort becomes more understandable. It is very typical of many or all parts of the world, that only a few kinds of

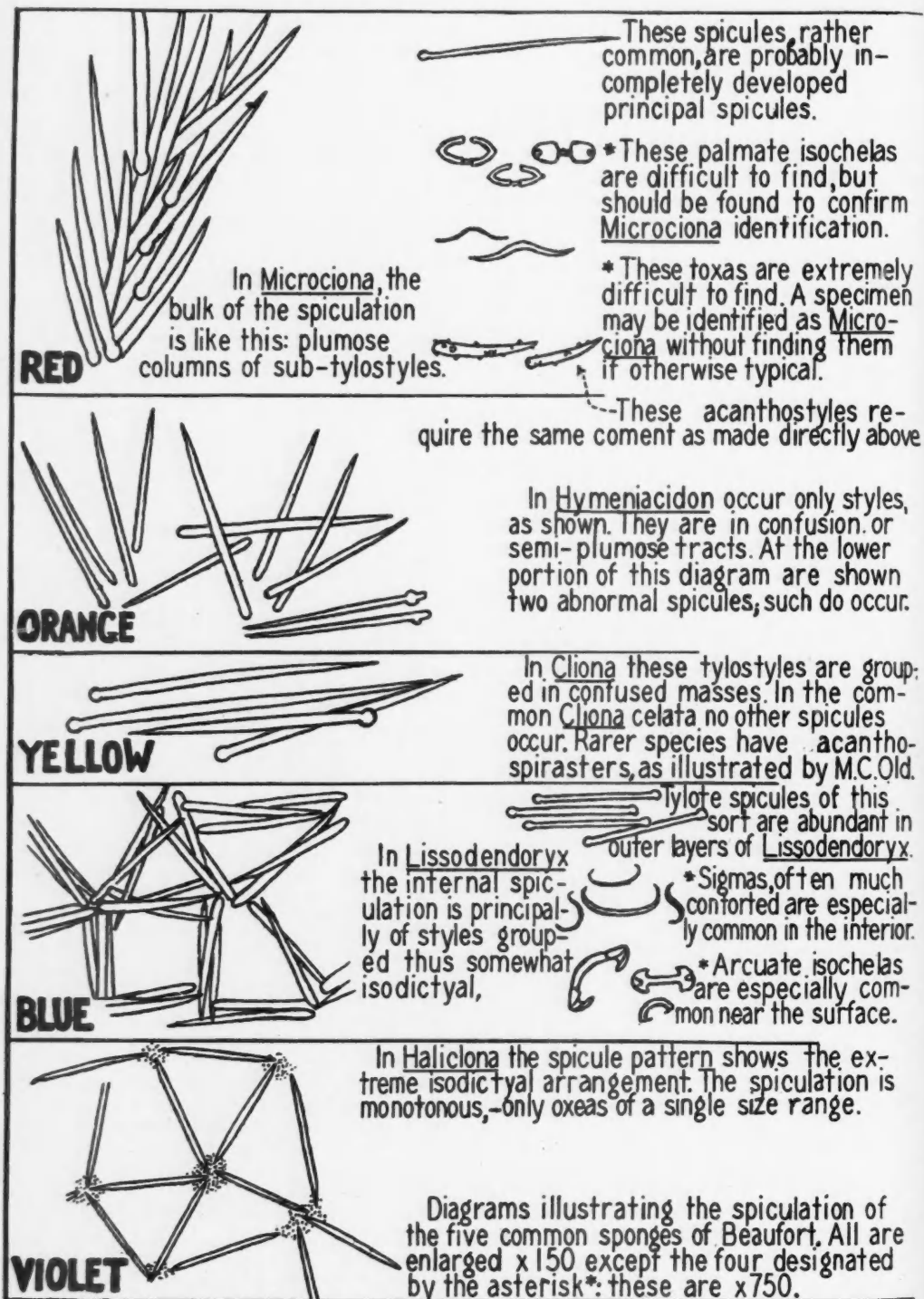


FIG. 2. Diagrams illustrating the spiculation of the five common sponges of Beaufort. All are enlarged x 150 except the four designated by the asterisk *: these are x 750.

sponges occur where they are drastically exposed to weather by low tides. Over and over again, as the author has personally observed in many parts of the world, in such places there are five of the following six: *Cliona celata*, *Haliclona permollis*, *Halichondria panicea*, a *Lissodendoryx*, a *Hymeniacidon*, and either a *Microciona* or some very closely related and similar appearing sponge. This is almost exactly the Beaufort fauna, except that the *Halichondria* is missing, and it is the rule that some one of the six is absent from each location where the other five occur.

It may be emphasized that the ecological situation at Beaufort Harbor favors those sponges that are normally intertidal, especially those which are typical of the upper portion of the intertidal area, but that it is severely inimical to the much more numerous species of Porifera which flourish only at or below the extreme low tide mark. If a sponge cannot endure exposure to rain (freshwater) it cannot endure Beaufort Harbor.

PHYSICAL ECOLOGY

The physical environment is altogether a matter of blows; the organism is struck by rays or by particles. The gross blows of large particles are often overlooked, but they deserve prior (even if brief) notice.

Sponges conspicuously do not grow where they may be stepped on, or where stones or other debris may roll on them. Where objects are tossed about, sponges do occur down in the cracks, but not in exposed situations.

Currents constitute a sort of buffeting, whether or not they produce results by obviously moving large objects, such as stones and sand. They may affect a sponge in several ways.

ANTAGONISTIC

- (a) Dislodging parts, or all.
- (b) Deformation, with internal injury.
- (c) Bringing smothering sediments.

BENEFICIAL

- (a) Bringing food and oxygen.
- (b) Removing waste products.
- (c) Washing off sediments.

Violent storms occur at Beaufort during winters. Dr. H. F. Prytherch reports that at such times numerous sponges, especially *Hymeniacidon*, are torn loose. It is well known that sponges are often tossed up onto beaches following storms, obviously newly dislodged from their submarine habitat.

It may be, however, that the sponges thus dislodged had almost or quite lived out a life cycle. It is surmised that some sponges are "annuals." Certainly the rule is that many specimens withstand these storms, so that each species continues to flourish.

Currents certainly modify sponge shape. One may notice where rocks are pounded by surf, that the sponges are regularly of the encrusting habitus. Else-

where some of the same species may have the same shape, and give indication that such is the inherent tendency of the species, but many kinds of sponges, when in calmer waters, reveal their inherent tendency to proliferate and to have a ramose or otherwise erect shape.

It is a matter of negative, but important observation, that sponges do not grow where sediments are rapidly building up the bottom. In fact, sponges very seldom occur on mud bottom at all. One of the few so to occur is *Craniella*. It is interesting to note that George & Wilson found a *Craniella* in Beaufort Harbor, but that now it seems to have disappeared from there; recent human activities (such as channel-deepening) have probably been to blame.

K. D. McDougall (1943) gave interesting data on currents at Beaufort. He found flood tide currents about half a mile per hour, ebb tide currents about twice this. The difference is due to the continual outward current from the rivers that empty into the bay. There are very few minutes of calm at the turn of the tide, almost instantly the current sets in at the new direction. McDougall's apparatus was set up at the Duke University Pier. Sponges grow much more abundantly on the pilings of the highway bridge, and of the railroad bridge. It is the author's observation that the currents at these two latter stations certainly reach a speed of at least two miles an hour (3 km.).

That currents are vital to sponges is borne out by the negative but important evidence, that the records lack instances of sponges growing in completely stagnant water. On the other hand, sponges are commonly found, in abundance, where surf beats hard, and currents are obviously violent.

That currents are vital to sponges is further shown by the results when efforts are made to grow, or even to maintain Porifera in running sea water aquaria. Sponges die very quickly if merely left in stagnant sea water. They live a little longer if a current of fresh sea water is continually arriving. They live still longer, at least roughly in proportion as the current has greater speed and volume. Precise figures are difficult to give, because it has so far been impossible to determine the precise instant that a sponge dies. One must wait until the odor of bacterial decomposition tells the story. It is clear, however, that the general principle exists as here described.

The juvenile sponge is free-swimming. Currents may dictate where and how successfully these larvae attach. McDougall points out (page 360) that plates submerged for two weeks at Beaufort, some horizontal and some at 45° from horizontal, received on their upper surface a "layer of fine mud and sand to the thickness of an inch or more." He quotes Pomerat & Reiner to the effect that "a sponge" settled in larger number on the under surfaces of submerged, horizontal plates, than on upper or vertical surfaces. McDougall found abundant sponge larvae attaching on under surfaces, too, con-

firing and amplifying this. McDougall's sponges are identified (*Haliclona* and *Microciona*).

It is the observation of the author, in the field, in many parts of the world, that sponges very rarely grow on upper surfaces, more often do grow on vertical surfaces, and most vigorously of all on under surfaces. Yet on the other hand, in the West Indies (near the Dry Tortugas) where very few under surfaces are available, sponges do grow in great abundance.

McDougall on page 362 reports findings for attachment of larval *Haliclonas* in five different artificial channels. He so arranged these that the current ran fastest through Number 1, and graded down to slowest in Number 5. The apparatus was merely suspended in the bay, Number 1 practically unhampered, the other four increasingly limited, so that there was barely any current at all in Number 5. Because the current varied with the tide in all, although absolute speed was not effectively studied, comparative speeds were measured. The speeds of the five are to each other, beginning with Number 1, as 12:9:5:3:1. The abundance of *Haliclona* attachments was 84:168:212:171:90, showing an optimum for the median current. The average size in millimeters of the young sponges gave nearly the same results; these sizes were respectively 6:14:12:11:8.

It must be noted that whereas success in attachment is important, some attachments being vital, it is more important to consider those items that permit maturity. Some animals made attachment with difficulty and in small numbers, yet grew so greatly that eventually they dominated the environment over others that had made more promising beginnings. It may be, for example, that the fewer larvae that manage to attach in places of stronger currents may yet live long and grow large, whereas the larger number of larvae that manage to attach in places of weaker currents may soon perish. Observations in the field tend strongly to confirm this hypothesis.

The physical environment often consists of more subtle blows than those of rolling stones, waves, and winds. Vibrations are very important, especially molecular vibrations or heat.

Temperatures of the water around Piver's Island are given for the years 1922 to 1928 inclusive by Gutsell (1931), who was studying Pecten. He records a minimum of 3° Centigrade (January 1927) and a maximum of 33° (August 1926). The intertidal sponges must be affected by air temperatures at low water, and air temperatures occasionally sink below the freezing point of fresh water, in winter.

On July 25, 1946 a study was made of the temperatures inside sponges (*Hymeniacidon*) as compared to air and water temperatures. This was at low tide, and concerned sponges that were exposed to sunlight. The lower end of the thermometer was forced into sponge tissue until the mercury-filled bulb was well concealed. The results were: air temperature, 29° C.; water temperature, 29° C.; sponge temperature, 33° C.

Typical marine sponges may succumb to water temperature as low as 12° to 18° (de Laubenfels 1932) but Lundbeck's many reports on Arctic sponges shows them thriving in sea water that was below the freezing point of fresh water. The endurance of cold which is exhibited at Beaufort is not astonishing. As de Laubenfels (1932) shows, marine sponges may readily tolerate temperatures over 35°, therefore the heat toleration which is shown at Beaufort is also commonplace.

Vibrations may be thought of as including the electromagnetic series, of which light is much the most studied by many ecologists. Infrared is studied in connection with heat, the Hertzian (very long) and the very short waves from the Schumann region on down (such as Roentgen and Gamma) are either absent or rather uniformly distributed in nature. Ultraviolet, while actually different from light, is sometimes spoken of as a kind of light, and usually is studied along with visible radiation.

Value of light to some fresh water sponges was well shown by the epoch-making article on sponge physiology by Van Trigt in 1919. The value of light to some marine sponges was shown by de Laubenfels (1932). Yet many sponges grow in total darkness. The sponges of Beaufort show noticeably greater abundance in areas of moderate illumination.

Hymeniacidon heliophila was well named by Parker. Among all the sponges of the world, it is outstanding for its occurrence in full sunlight, out of water. There are areas of as much as fifty consecutive meters in length of shoreline, where conditions seem to the thoughtful observer to be exactly like other localities where *heliophila* abounds, but where there are no specimens of this species; these are strongly illuminated areas. Yet in equally bright areas, apparently in no way different, *heliophila* specimens may occur up to seven per linear meter. In shaded areas, such as beneath bridges, it is common that there should be twelve to sixteen specimens of *heliophila* per linear meter. Thus even this species shows what may be called a preference for modified illumination.

The Beaufort sponges, other than *Hymeniacidon*, are definitely uncommon in full sun, but may occur where such exposure occurs for part of the day.

McDougall studied the quantity of attachments made by larvae of *Haliclona* in areas of six different amounts of light. His chamber Number 1 had nearly the normal illumination that obtains under water, very near the surface. Each higher number was darker, up to Number 6, which was almost totally dark. The sponge larval attachments were: 1, 11; 2, 17; 3, 18; 4, 23; 5, 15; 6, 20. This does not seem to indicate any pronounced phototaxis. Nor would any such taxis settle the question of where adult sponges can thrive, because many might attach themselves to areas where they later would perish, and a few attach at areas where they would later live long and prosper.

In conclusion to these remarks about physical en-

vironment it should be observed that none of them offer a satisfactory clue to the lack of deeper water sponges, which lack is so conspicuous near Beaufort.

CHEMICAL ECOLOGY

Chemical effects of environment are probably very important at Beaufort. Much of the time the water is browish, like iced tea, as a result of solutes leached from the humus and leaf mold of the forest floor which is drained by the tributary watershed. These organic substances may have a nourishing effect, or may be toxic. It is possible that some species would react to them in one way, others in the opposite way. They require further investigation.

The alkalinity or pH should be studied carefully at Beaufort. Does it vary greatly from time to time and place to place? Is this correlated with the success or failure of various organisms? This warrants investigation.

The principal chemical effect that has been carefully studied at Beaufort concerns total inorganic salts present, or salinity. From this standpoint, the Beaufort area must be regarded as emphatically brackish. Gutsell (1931) records the following extreme fluctuations in parts per thousand:

	max.	min.
January	35	14
February	35	16
March	34	18
April	35	15
May	35	23
June	37	22
July	38	21
August	38	21
September	37	6
October	35	14
November	38	16
December	35	14

The summer of 1946 was one of exceptionally severe rain and low salinity. The author found salinity as low as 15 parts per thousand in July, 1946—much lower than Gutsell's lowest record for that month. The further observation can here be added that the salinity varies but little from place to place around Piver's Island, from bottom to top (McDougall made an observation to this effect on page 330 of his monograph) and from low tide to high tide. The range for the latter was found by the author to be only about 4 parts per thousand. Clearly the large expanse of shallow water over which the incoming salt water is distributed favors complete mixing as compared to a deeper narrow channel in which cooler or saltier water might sink and stay down.

The phenomenally low salinity of only 6 parts per thousand, which occurred in September 1924, gave many indications of being fatal to large numbers of plants and animals normally present, so that

a slow return to normal population followed; in fact, it may be that some forms have not yet returned to their previous abundance near Beaufort. A freshet bringing these waters to a point as nearly fresh as that, constitutes something of a disaster.

Attention should be called to the fact, pointed out by McDougall and others, that summer is the time when sponges normally flourish most. It is clear from the record that it is commonplace to have salinity sink below 2‰, but that when such sinking occurs in winter it may be classified as a "normal hazard." The summer freshet is more serious.

The freshet of early July, 1946, certainly seemed to be injurious to sponges. The *Haliclonas* were altered in color at once; for some weeks thereafter only dull, drab individuals could be found. This is the color to which *Haliclona* turns when dead. It would seem that some life remained in the masses of sponge tissue, however, because in August the violet color began to reappear. It was still very difficult to find any large specimens. Judging by reports of other observers for other years than 1946 it becomes clear that the total growth made by this sponge was curtailed by the freshet.

After the freshet many of the *Hymeniacidons* exhibited unusual colors, probably as a result of it. Almost all assumed a darker, more brownish color than normal. Dead specimens of this sponge turn the same dark brown. That few or none of them really died is borne out by the observation that by the first of August all had gradually resumed the normal bright orange color. It is probable, however, that a period of delayed growth occurred. Specimens were studied as they occurred in the field, and throughout the most of July no increase in size could be detected. It may be assumed as probable, that normally they would have grown considerably in that month. How was the somewhat darker color arrived at? An hypothesis was considered, that there might be a scattering of dead cells, each with the dark brown color that is characteristic of completely dead *Hymeniacidon*. Microscopic study refuted this assumption. Of the cells containing the spherules that are responsible for the sponge's color, all had spherules of the same color, and no obviously dead cells could be detected.

In most summers (but not 1946) the creeks that empty into the waters about Piver's Island, run low. With this shortage of incoming fresh water the effects of evaporation become evident. Inside the banks that shelter Beaufort are many square miles of very shallow water, less than a meter deep. In hot, dry weather this sponge-inhabited water is therefore often of a greater salinity than occurs in the open ocean.

During dry summers, some of the many marine sponges may begin to immigrate, as indicated by the records of George & Wilson; but these small patches of miscellaneous marine sponges cannot be regarded as permanent or normal members of this fauna.

The point may be made, however, that high salin-

ity, such as sometimes is found at Beaufort, is obviously not fatal to sponges.

The marine sponge *Iotrochota* was studied for salinity effects by de Laubenfels (1932). Using cellular material, this species was found to take serious damage and soon die at salinities less than 20 parts per thousand, and at salinities greater than 40 parts per thousand, but within the range of 23 to 38 parts per thousand there was a high, almost complete toleration. Such a sponge would endure the highest, but not the lowest Beaufort salinities; the records of occurrences of Porifera indicate that most marine sponges resemble *Iotrochota* in this regard.

There are comparatively few records of sponges occurring in brackish water. The fresh water sponges, especially *Spongilla*, are well known so to occur. Annandale (1915, page 1 and following) discusses this fact, and also the occurrences in brackish water of *Craniella dactyloidea*, *Cliona vastifica*, *Suberites sericeus*, *Laxosuberites aquaedulcoris*, and *Laxosuberites lacustris*. The first two genera, as has been already noted, also occur in the brackish waters of Beaufort. The *Suberites* is otherwise exclusively marine. The species of *Laxosuberites* mentioned by Annandale were found only in brackish water. Species of *Haliclona* are known to occur in Lake Baikal, which is now fresh water. Their relatives are salt water sponges; this and other criteria indicate that Lake Baikal was once in communication with the ocean. Presumably it went through an intermediate brackish stage, which the *Haliclonas* endured.

Burton (1926) reported on sponges of the vicinity of the Suez Canal. He gives the collecting station references without comment on salinity, but these stations are described on page 45 of the general part. Thus one discovers that *Haliclona permollis*, *H. tabernacula*, *Tedania assabensis* and *Hircinia variabilis* were in brackish water. Two of these species occur also at Beaufort.

There are in the world approximately a thousand genera of sponges. Of these, some twenty-five are composed of species which occur in completely fresh water, and seven or eight others contain species which occur in brackish water. An additional five genera, which are of great importance in the Beaufort Harbor fauna (and perhaps as many as five more which do not occur at Beaufort) contain species which can endure low-tide conditions, including frequent exposure to the air, and thus to fresh water (rain) or to brackish water (Beaufort). At least 97% of all sponge genera are completely confined to environments which have the salinity of normal seawater.

It may be well at this point to review two observations. The sponges (such as those abundant in Beaufort Harbor) which can endure intertidal environments cannot well endure immersion in brackish water throughout the twenty-four hours, as shown by their comparative absence below low tide. Second, they endure fresh or brackish water at a price, with

a necessary period of recuperation, as indicated by observations at Beaufort in July, 1946.

An hypothesis may be suggested, for further investigation, that sponges which are usually or normally adjusted to salt water, but which are able to endure temporary exposure to fresh or brackish water, must have a daily period of being exposed to air.

A simple, inconclusive, but suggestive experiment was tried. Hymeniacidon material was collected, all at the same point. Half of it was kept continually immersed in a running seawater aquarium. Half was kept on a board, in the air, but dipped in seawater several times a day. The first was obviously dead in three days, the second still alive at the end of six days. Not all the factors were well controlled, but the indications do tend to confirm the hypothesis. Perhaps an extra rich oxygen supply is needed if a sponge is to survive in spite of low salinity.

Cliona does occur below low tide at Beaufort. Oysters growing below low tide give the optical impression of being more extensively eroded by boring sponges than oysters growing above low tide. Dr. Prytherch states that this observation is generally made by practical oyster fishermen as well as independently by the author. Quantitative data doubtless could be amassed.

Yet *Cliona* offers a striking difference between individuals which grow below tides at Beaufort as compared to individuals which grow below tides in fully marine environments. In the latter, but conspicuously not in Beaufort Harbor, the boring sponge continues to grow until it forms a large, sulfur yellow mass, out of the shell in which it began. Soon the original hidden tissue is but a minute fraction of the total. On August 24, 1946, specimens of *Cliona* of this massive type were collected in the open ocean near Beaufort.

It is quite likely that the partial success of *Cliona* under brackish water may be due to the boring habit. At first glimpse one would surmise that the sponge excavated and hid to escape being eaten, yet it is a matter of common observation that few animals will eat sponges. Further study indicates that *Cliona* bores to escape fresh or brackish water.

A simple, inconclusive, but suggestive experiment was tried. *Cliona* (in oyster shell) was dipped briefly in completely fresh water, then left in salt water. The early appearance of odor indicated that it had been promptly killed. Of course, this is not well controlled, and death may have been due to other causes. Yet a control kept continuously under ordinary Beaufort water (somewhat brackish) survived at least five days. The indications do tend to confirm the field observations.

It must be stressed that for definite results, this experiment should be carried out with some better criterion of when death takes place than the extremely vague indications relied on in 1946. Yet it is here surmised that *Cliona* really is very vulnerable to completely fresh water, even when it is

buried within its excavations. It is obviously resistant to brackish water when so buried, but not very resistant even to brackish water when not so buried.

The oxygen-carbondioxide relationships of sponges have not been adequately studied, but they seem to be relatively simple. The remarks about currents, given in the discussion of Physical Environment, undoubtedly bear upon the gas content of the waters and the results to any sponge. The indications are that Porifera have rather high requirements for oxygen. Van Trigt (1919) and de Laubenfels (1932) have shown photosynthetic relationships for sponges. This is doubtless significant in terms of oxygen need, but it touches upon the following topic, too.

BIOLOGICAL INTER-RELATIONSHIPS

Sponges as a phylum are notably involved in symbioses. Many of them are packed with microscopic plant cells, often the very small cells of little-known Myxophyceae. No cases are known of sponges being parasites, consuming the protoplasm of still-living victims, but many sponges are commensals or riders on such animals as crabs or hermit crabs. A few animals eat sponges, notably certain of the nudibranch mollusks (Gastropoda).

1. *Microciona* is seldom found growing other than on the shells of other invertebrates; this is especially true in the vicinity of Beaufort. Whenever one sees what seems to be a particularly plump specimen of this species, he is apt to discover that he has a handful of mostly barnacle shells, rather thinly coated with sponge. The barnacle may still be alive, able to stretch its appendages out through windows in the *Microciona*, but often the barnacle is dead.

It is clear that sponges are a chief enemy of barnacles. Other colonies, such as Bryozoa (commonly) and even hydroids, grow laterally, so that they smother barnacles, but sponges do this to a very great degree.

Microciona grows very commonly on oysters, as Rafinesque observed in 1818. Yet no evidence was found by the author that the oyster was ever damaged. The oyster's method of opening and closing its shell is evidently adequate to keep a channel open, and the mollusk can obtain its required water circulation through this aperture. In fact, it is evident in the vicinity of Beaufort that where *Microciona* is especially common, that is to say—the environment most suitable for it—that oysters are likewise large, abundant and obviously thriving. This might well be called the "oyster sponge" as Rafinesque proposed.

2. *Hymeniacidon* shows much less tendency to smother other organisms than is shown by many sponges. It does grow laterally, and thus sometimes has the smothering effect, but to a relatively great degree it grows at about right angles to its base of attachment. It commonly attains lengths in this direction of about 10 cm.

All sponges are penetrated by other animals. It is difficult to say in particular cases, whether or not

these invaders are eating the sponge, or whether they are merely using it as a home. The large "logger-head" sponge (*Sphecospongia*) which grows offshore from Beaufort, has very large inhalent canals, from which the very small pores open to the active sponge tissue. These canals are regularly inhabited by shrimps, which do not eat the sponge, however, but merely live from their sieving of the water currents.

Hymeniacidon is host to immense numbers of very little animals. Several sponges of this sort, aggregating 800 cc., or about the size of a grapefruit, were placed in a dish and allowed to become stagnant. As a result, probably of lack of oxygen or food, small animals came streaming out of the sponge's cavernous interiors. Within two hours the bottom of the dish exhibited:

Large nematodes—(visible to the unaided eye)....	50
Microscopic nematodes	1,000
Macroscopic annelids	100
Microscopic annelids	200
Macroscopic amphipods	500
Microscopic amphipods	800

This meant that there were at least three such inhabitants for each cubic centimeter of sponge. It is practically certain that at least some of them, especially the nematodes, were parasites. It is remarkable that a sponge can continue to seem healthy, to grow and prosper, in spite of being thus victimized.

Study of stomach contents of some of these worms was attempted, in an effort to determine for certain if they were parasitic. The small size made this impractical; evidently, if they do eat the sponge, they ingest about one cell at a time, and quickly digest it.

Some specimens of *Hymeniacidon*, growing in good illumination, contain small green cells, evidently plant symbionts. This condition is exceptional, however, and if this sponge depends extensively upon plant cells for help, it must be upon other than the obviously green ones.

3. *Cliona* has a number of ecological relationships that other sponges do not have, and lacks many of theirs. This situation arises from the well-known fact that for at least the early part of its life, *Cliona* burrows into calcareous material, which very often is oyster shell. In the vicinity of Beaufort, the relationship of *Cliona* and oyster is an economic problem, and men in the business of collecting or raising oysters agree that *Cliona* is one of the principal causes of loss. To be sure E. P. Churchill says (1920, page 40) of the boring sponge "it does not occur in sufficient numbers in most regions to prove a serious menace," but the implication is clear that in a minority of regions it is serious. Furthermore, Churchill makes this pessimistic statement on the same page: "no means of protections against the sponge can be suggested." M. C. Old (1941) refers to the ruin of the oyster business in 1934 in the Little Choptank region of Chesapeake Bay by *Cliona*. Means of protecting oysters are to be desired.

As the sponge buries itself deeper and deeper, it does not actually enter the flesh of the mollusk, but comes so close to doing so that the shell is seriously weakened, especially when the sponge's burrows underlie the points of attachment of the oyster's adductor muscle. This weakening serves as a stimulus to the mollusk to build up more shell. This building is a drain on its energies, and keeps it from being as large and succulent an item of human diet as it would otherwise become.

The relationships of *Cliona* to fresh water were mentioned above, in discussing the chemical environment; it is very probable that the sponge burrows to escape danger of fresh water exposures, to which it is certainly otherwise vulnerable, and probably somewhat vulnerable, even so.

Churchill reports, in contrast, that oysters endure exposures of a day or so in salinities as low as 5 parts per thousand, and that oysters thrive in salinities between 16 and 32 parts per thousand. H. F. Prytherch reports that the brackish-water-tolerant oysters gain as a result of freshets, because the low salinity reduces *Cliona* infestation.

Further confirmation of the theory that fresh water can help oysters by deterring their enemy, the boring sponge, is afforded by ecological observations at Beaufort. It is obvious even to the casual visitor that the intertidal area is crowded with oysters—so packed that oysters grow attached to yet other oysters—layer upon layer until the buried layers are smothered. On the other hand, immediately below low tide, the abundance of oysters falls off sharply.

In his study of the attachment of marine invertebrates at Beaufort, McDougall comments (page 369) on the great abundance at that vicinity of larval oysters. This is confirmed by Dr. H. F. Prytherch. McDougall points out that enormous numbers of these larvae attach below low tide, while only a few become affixed between tide marks. He provided square tiles of uniform size 7.5 by 15 cm. in surface area, for such attachment. On page 342 he records over 125 oyster "spat" per tile at depths of one meter below low tide, nearly a thousand per tile at $2\frac{1}{2}$ meters depth, but many intertidal tiles had none at all! Only on a few tiles exposed a long time intertidally, did any young oysters at all attach. But he goes on to say of the area between tides: "yet ultimately all those below this region were eliminated and the final population was wholly intertidal." He speculates, without data, as to the reasons why the continually submerged oysters die at Beaufort. He suspects the oyster drill (*Urosalpinx*) a snail that perforates oyster shells, and eats them. It must be noted, however, that this gastropod also readily invades the intertidal zone. He also suspects "incrusting organisms" and specifically suspects *Cliona*.

Means of protection against the boring sponge can be suggested, but the expense of some suggestions may well be so great that they are not feasible.

A first suggestion is to copy the French method.

Hugh M. Smith in the *National Geographic* for March 1913 describes how in that country oysters are reared artificially on trays, handled repeatedly by human labor. Spraying with fresh water is but a minor addition to the extensive routine. Needless to say, *Cliona* is not a major problem to the French oyster cultivator. The cost of labor in the United States is so great, however, that the European method is not practical.

The Japanese method is worth considering. Smith also describes their oyster farms: First, they raise the oysters (with little handling) on a substratum of branches of bushes. Second, they keep the oysters intertidal, so that rains at low tide suppress the growth of *Cliona*. Experiments have been tried in America, using brushwood as attachment or "cultch" for oyster set, and although the results were good, branches were abandoned in favor of old oyster shells. These experiments should be repeated more extensively.

Near Beaufort, many square miles of shoals are completely or almost bare at low tide. Such an area might be surrounded by a high fence of woven wire and filled with brushwood anchored by wires. Oyster sets could grow on the bushes.

4. *Lissodendoryx* might almost be called an "interstitial sponge." It is rather difficult to obtain a continuous piece of this species that will be as large as a watch; one must usually collect it in peanut-sized fragments or finger-sized strands. Yet it covers perhaps 5 to 10% of many pilings, intertidally, near Beaufort. It is hidden under plumose hydroids and bryozoans, around the bases of ascidians, and over barnacles. To all appearances, only barnacles are actually smothered by *Lissodendoryx*. Other sessile invertebrates seem to grow through it, or rather to be able to tower over it, so that they carry on in spite of it; it cannot seem to clear a space for itself, as do *Microciona* and *Haliclona*. Nevertheless, although thus shaded, the sponge seems to thrive. In the West Indies, the author has found *Lissodendoryx* growing in nearly full sunlight. Its range of tolerance is large.

The evil odor of *Lissodendoryx* may keep some enemies from eating it, but it does not discourage the small animals that inhabit it. An aggregate of 900 cc. of this sponge was put in a dish, and allowed to become stagnant. The fauna that was thus forced out, into the bottom of the dish, included:

Macroscopic nematodes	100
Microscopic nematodes	2,500
Microscopic annelids	200
Macroscopic amphipods	500
Microscopic amphipods	1,500

There were thus at least 5 such inhabitants for each cubic centimeter of sponge. Many of the amphipods were of the genus *Caprella*.

It is the rule, with very few exceptions, that the dermal layer of *Lissodendoryx* is loaded with greenish or bluish spherules. The vegetable nature of these can well be surmised, but the whole problem of

sponge-algae symbiosis is one to challenge the botanist who specializes in micro-organisms.

5. *Haliclona* is that one of the Beaufort sponges which is the most available for report in McDougall's masterly monograph. Young individuals of this sponge made attachment abundantly on the tiles which he kept in the water near the south end of Piver's Island (Duke University Pier). He describes these young sponges (page 331) as greenish-yellow translucent patches. The first ones appeared early in June. By the middle of June, for each tile put out in the water, an average of 30 *Haliclonas* attached. Tiles put out from that time on, acquired fewer *Haliclonas*. Tiles put out the first of July acquired only four apiece, and tiles put out after the middle of July received no sponges.

McDougall actually observed *Haliclona* juveniles smothering out other young animals that were also trying to get a start in life; he noted as victims barnacles and tube-dwelling annelid worms.

All over the world (in intertidal areas) encrustations of *Haliclona permollis* take up space. It is obvious that where the sponge is absent, other organisms would instead occupy that area. Thus the list of animals engaged in antagonistic relations with this species is the whole list of the many sessile, intertidal invertebrates; a most imposing assortment indeed. It is obvious that *Haliclona* copes with these others efficiently.

Haliclona encrustations may be described, in comparison to some other sponges (especially *Lissodendoryx*), as being "clean." Other macroscopic plants and animals are practically absent from the sponge's area. In part this points to rather small ability to grow over and so smother large organisms. It appears from field observation that when *Haliclona* arrives by lateral growth against another sponge, sea anemone, ascidian or against nearly any comparatively large animal, the sponge is baffled and stops. Under similar circumstances *Halichondria* (not present at Beaufort) makes extensive vertical growth, often becoming pillar-shaped. *Haliclona* does then grow more vertically than usual, but not so pronouncedly. This brings up the matter of "tubes" or oscular walls.

Haliclona thrives in surf-pounded areas, but there the oscules are surrounded by walls that are often less than a millimeter high, whereas the oscules are 2 to 5 millimeters in diameter. It will be obvious to note that the water currents very promptly remove the noxious out-pouring from the oscules, so that there is very little danger of its re-entry into the pores; which inhalant apertures are distributed in great abundance over nearly the whole surface of the sponge.

Haliclona also lives in areas of rather little current. It has been already noted that McDougall found some young ones in his current boxes "Number 5," in which the water movement was barely noticeable. But in areas of less current the oscular wall rises higher—often 6 to 10 millimeters. Obviously, like the smoke stacks of steamers, this structure leads

the noxious output away. This species has been given the colloquial name in California of "Lavendar volcanoes."

In crowded situations on the pilings at Beaufort, the oscular tubes at times reach heights of several centimeters. This species *H. permollis*, grows thus in similar ecological situations in other parts of the world. George & Wilson make no comparison between their specimen and specimens of *permollis*, although they do point out differences from sixteen other described species. Yet the name they chose as for a new species, "*tubifera*" indicates that they were impressed by these proliferating specimens. The author found many specimens, even on the pilings at the railroad bridge, that were typical in all respects of the "Lavendar Volcano" shape so common for *H. permollis* in other localities.

Some specimens of *Haliclona permollis* are rather blue than violet. These contain great numbers of a vegetable cell that was readily observed with the high power of the microscope. It is probable that smaller vegetable cells are even more generously distributed among sponge specimens and species. The symbionts now under discussion were elliptical masses of jelly 6 microns in diameter by 10 microns long. In each occurred what was either a large chloroplast or the cell proper; these were elliptical olive-green bodies 4 microns in diameter and 7 microns long. These plants were often aggregated into rows, chiefly single file, but here and there two might lie side by side in the series. Two West Indian species of *Haliclona* were described by de Laubenfels (1932) as containing symbiont Myxophyceae.

SUMMARY

Beaufort Harbor and vicinity is notably devoid of sponge life below low tide mark, probably because occasional freshets cause the water to become decidedly brackish. Intertidally there are very numerous individuals of five species of sponges. These represent five genera which are typical of intertidal environments all over the world.

Preliminary investigations and numerous field observations indicate that these sponges are helped by currents, even very vigorous ones. They endure temperatures from about zero to at least 33° C. Sponge tissue may be upwards of 4° degrees warmer than air and water temperatures when in full sunlight. In general, partial illumination seems to be better environment than full sun.

Low salinity may cause damage, but the intertidal sponges can recover from its effects. Ninety-seven percent of sponge genera, however, are restricted to water of full salinity (3.5%). There is evidence that the boring sponge, *Cliona*, hides in calcareous material chiefly to escape exposure to low salinity, and oysters may possibly be protected from *Cliona* by dousing with fresh water.

Sponges, other than *Cliona*, render little or no damage to oysters, but do over-grow and smother many other sessile invertebrates, especially barnacles.

Sponges are inhabited, and probably damaged, by very numerous nematodes, annelids, and amphipods. Many sponges contain microscopic plant symbionts that are probably beneficial.

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BIOLOGY OF THE ISOPODA OF MICHIGAN

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BIOLOGY OF THE ISOPODA OF MICHIGAN

INTRODUCTION

Although the order Isopoda is a well-known group, scattered over much of the world, and has attracted the attention of many workers, little is known concerning the distribution and life history of most species. Marine isopods have been more thoroughly studied than have the terrestrial and fresh-water representatives. The species of Europe have received considerably more attention than have those of America. In fact, most papers concerned with these crustaceans have been written by European workers, while comparatively few have appeared that dealt with the American fauna. Within the American literature, most contributions have been concerned with taxonomy. Many questions, however, on other aspects of the biology of this group remain to be answered. Because of scarcity of distributional data, limits of the ranges of most North American isopods are still to be determined. Relationships between American and European species have not been clearly established. The ecology and natural history of these animals are fields in which further research is seriously needed.

The literature dealing with the order Isopoda is very extensive. Linnaeus described several species, some of which are still valid today. Thomas Say (1818) was one of the first American systematists to work with these animals. There have been, however, few workers primarily interested in the isopods of this continent. Most of the research on these crustaceans may be classified into three major divisions: taxonomy, morphology, and experimental zoology. Few workers have been concerned with their distribution, ecology and life history.

The objectives of this investigation were to determine: (1) what are the isopods of Michigan; (2) what is their distribution within the state, particularly in the lower peninsula; (3) what are the habitat preferences of the terrestrial species; (4) what are the salient features of the life history of common terrestrial isopods; and (5) what are the variations in sex, size and other biological phenomena to be found by quantitative analyses of an isopod population in nature.

Field study began in the summer of 1938 and continued through August, 1942. Intensive work was done in Washtenaw and adjacent counties in the south, and in Cheboygan and nearby counties in the northern part of the southern peninsula. However, it was not possible to make intensive collections over the entire state. Neither was it feasible to include much of the upper peninsula within the region in which isopods were studied. During the course of this investigation, 359 new locality records for isopods were established from 74 of the 83 counties in Michigan. The remaining nine counties are all lo-

cated in the upper peninsula, and there are published records from two of them (Adams 1909, Hatch 1939). Fifteen species of isopods are now known to occur in the state. Four of these are reported from Michigan for the first time. There have been few records published for the other species in this state.

I am indebted to numerous persons for their cooperation throughout the investigation, and wish to convey my sincere thanks to each of them. This work was directed by Prof. Frank E. Eggleton, and to him I express gratitude and appreciation for his help and inspiration. Special thanks are also due to Mr. James O. Maloney of the Division of Marine Invertebrates, The United States National Museum, who checked some of the identifications; to the University of Michigan Museum of Zoology and particularly Dr. K. E. Goellner for permission to study specimens from their collections; to Mr. Harry H. Wileox, Jr., who drew Figures 1-14; to Dr. F. C. Gates for meteorological data; and to the Director for use of facilities at the University of Michigan Biological Station. The collecting trip in the spring of 1942 was financed in part by a Grant-in-Aid from the Horace H. Rackham School of Graduate Studies of the University of Michigan.

DISTRIBUTION OF MICHIGAN ISOPODA

Although the origin and world distribution of the isopods known to occur in Michigan have not been definitely established, certain general statements can be made. As far as is known today, all aquatic isopods of the state are restricted, in general, to the eastern part of North America. Among the terrestrial species, *Ligidium longicaudatum* Stoller and possibly *Trichoniscus demivirgo* Blake probably are to be found only on this continent. The remaining terrestrial species occur in Europe as well as in this hemisphere, and Van Name (1936) states that they may have had their origins in the Old World.

One of the earliest works that dealt with the Isopoda of North America was Say's, "An Account of the Crustacea of the United States" (1818). Richardson's "Monograph on the Isopoda of North America" brought up to date the literature published prior to 1905. Van Name (1936 and supplements 1940, 1942) reviews the taxonomy and distribution of isopods of the entire Western Hemisphere. However, there have been few papers concerned solely with this order from definite sections of this continent—Longnecker (1924) for Iowa, Johansen (1926) and Walker (1927) for Canada, Blake (1931a) for the New England States, and Miller (1938) for California. Although all these regional papers are rather short, nothing even comparable to them has been written for Michigan prior to the present publication.

MICHIGAN RECORDS

Probably the first records of the isopods of Michigan are those in S. I. Smith's "Crustacea of the Fresh-Waters of the United States" (1874). Richardson (1905) added three species to Smith's records, but all her specimens were from Saginaw. Adams (1909) reports *Cylisticus convexus* (De Geer) from Isle Royale. One of the first papers to deal exclusively with the Crustacea of the state was Pearse's "A Preliminary List of the Crustacea of Michigan" (1910), which lists only six species of isopods; many of these had been reported previously by others. However, his paper of 1912 contains the first record of *Asellus intermedius* Forbes for Michigan. Pearse (1913) gives additional records from the state. Hankinson (1916) tells of taking *Mancasellus tenax* (Smith) from Chippewa County. Hatch (1939) records distributional data for six species from Michigan, and Dendy (1944) mentions a new locality for *Asellus communis* Say.

These published accounts of Michigan isopod fauna are the only records known to the author. In all, eleven species have been reported previously from the state. However, the records of these are sparse and in many instances a species has been reported from only one locality. A total of 28 records have been published previously for Michigan.

During this investigation, collections of terrestrial isopods were taken in all counties of the lower peninsula of the state. Two counties were selected in which to do intensive collecting. These were Washtenaw in the southern part of Michigan and Cheboygan at the northern tip of the lower peninsula. The ecology of these two areas is strikingly different. Washtenaw is highly agricultural, is well populated, and has a general loamy soil and deciduous hardwoods; Cheboygan County is generally not agricultural, is sparsely settled, has sandy soil, and its woods are largely aspen or coniferous. Although collections were made in the remaining counties of the lower peninsula, these were not covered as thoroughly as the two mentioned. The records from the upper peninsula are rather meager, since the author's interest did not lie primarily in that region.

Fifteen species of isopods, representing five families and ten genera, have been found in the state of Michigan. Of these 15 species, four are reported for the first time from this state. These are *Armadillidium nasatum* Budde-Lund, *Oniscus asellus* Linnaeus, and *Trichoniscus demivirgo* Blake for the terrestrial species, and *Mancasellus danieli* Richardson in the aquatic group. With the exception of *Mancasellus dilatus* (Smith), representatives of all these species were collected by the author or were identified by him in the collections of the University of Michigan Museum of Zoology. The following are the species now known for Michigan:

TERRESTRIAL SPECIES

Ligiidae

Ligidium longicaudatum Stoller

Trichoniscidae

Trichoniscus demivirgo Blake

Oniscidae

Oniscus asellus Linnaeus

Porcellio scaber Latreille

Porcellio spinicornis Say

Porcellionides pruinosus (Brandt)

Cylisticus convexus (De Geer)

Tracheoniscus rathkei (Brandt)

Armadillidiidae

Armadillidium vulgare (Latreille)

Armadillidium nasatum Budde-Lund

FRESHWATER SPECIES

Asellidae

Asellus communis Say

Asellus intermedius Forbes

Mancasellus tenax (Smith)

Mancasellus dilatus (Smith)

Mancasellus danieli Richardson

MICHIGAN SPECIES

The classification used in this paper follows that of Van Name (1936). Although many taxonomic problems exist in this group, the present publication is not concerned with them. As an illustration of such a problem, the differences between the number of articles in the first flagellum of *Asellus communis* and *Asellus intermedius* can be cited. Asellids with anywhere from seven to fifteen articles for each first flagellum are in my Michigan collection. These two species are usually separated from each other on this variable character. This situation will be discussed further in a later section, since it is also thought by some workers that these two species may not be distinct. However, in this publication, following Van Name, they have been treated as different. Many additional uncertainties exist in regard to the other freshwater species.

Inasmuch as the classification of the freshwater species is still not entirely settled, it was decided that it would be better to use characters for aquatic species as they appear in Richardson's monograph rather than to establish, at the present time, new distinguishing characters for use in the following key. Accordingly, the latter part of this key has been adapted from that monograph, making only such changes as were necessary to fit it to the fresh-water isopods of Michigan.

Characters used in the key, for the most part, are those plainly visible in properly preserved specimens. However, tracheae within the pleopods of terrestrial isopods are seen best in living specimens. A solution of nine parts 70% ethyl alcohol, one part glycerine, and a few milliliters of glacial acetic acid is an excellent preservative for isopods. In looking for tubercles and roughness on the body, it may be advisable to dry the specimens. Otherwise the animals should be observed when well covered with preserving fluid. Not all distinguishing characters have been given in the key for each species treated therein, rather, only the more conspicuous ones. For complete descriptions, as well as synonymies, of all isopods of Michigan see Richardson (1905) or Van Name (1936).

KEY TO THE ISOPODA OF MICHIGAN

1. (20) First pair of antennae inconspicuous, rudimentary and not one fourth as long as second pair. Abdominal segments distinct. *Oniscoidea*—Terrestrial Species2
2. (5) Uropods not extending beyond the terminal abdominal segment. (Fig. 11).....3
3. (4) Small median V-shaped notch in front of head (Fig. 5). *Armadillidium nasatum* Budde-Lund.
4. (3) Head not notched in front. *Armadillidium vulgare* (Latreille).
5. (2) Uropods extending beyond the terminal abdominal segment. (Figs. 6, 12, 13).....6
6. (9) Flagella of second antennae (first are rudimentary) 4 to many articles. (Figs. 7, 8).....7
7. (8) Flagella of second antennae 4 or 5 articles (Fig. 8). Inner branch of uropods shorter or equal to outer branch. Species small (3 mm.). *Trichoniscus demivirgo* Blake.
8. (7) Flagella of second antennae multiarticulate (Fig. 7). Inner branch of uropods longer than outer branch. (Fig. 6). *Ligidium longicaudatum* Stoller.
9. (6) Flagella of second antennae either 2 or 3 articles. (Figs. 9, 10).....10
10. (11) Flagella of second antennae with 3 articles (Fig. 9). *Oniscus asellus* Linnaeus.
11. (10) Flagella of second antennae with 2 articles. (Fig. 10)12
12. (13) Abdomen abruptly narrower than thorax (Fig. 13). Antennae conspicuously banded with white at joints. *Porcellionides pruinosus* (Brandt).
13. (12) Abdomen not abruptly narrower than thorax (Fig. 12). Banding on antennae absent or not prominent.14
14. (15) Dorsal surface of body strongly convex; smooth and usually shiny particularly on head. Capable of rolling into a ball. *Cylisticus convexus* (De Geer).
15. (14) Dorsal surface oval rather than convex. Head rough (Fig. 2) or tuberculated (Fig. 4). Cannot roll into a ball.16
16. (17) Dorsal surface of head rough, but not conspicuously tuberculated (Fig. 2). All pleopods furnished with tracheae. In males, the carpus (third segment from distal end) of seventh pair of legs with a prominent triangular keel-like expansion on dorsal border (Fig. 14). *Tracheoniscus rathkei* (Brandt).
17. (16) Dorsal surface of head with many conspicuous tubercles (Fig. 4). Only first two pairs of pleopods with tracheae. Seventh carpus of male not as above.18
18. (19) Dorsal surface of body conspicuously tuberculated. Tubercles on head very prominent. At least three color phases: solid dark gray, gray with lighter margins, and variegated. *Porcellio scaber* Latreille.
19. (18) Dorsal surface of body with small inconspicuous tubercles. Color, yellowish with gray-brown patches generally arranged in five longitudinal rows. If living, a double row of bright yellow spots along mid-dorsal line. *Porcellio spinicornis* Say.
20. (1) First pair of antennae plainly visible and at least one fourth as long as second pair. Posterior segments of abdomen fused. *Asellota*—Freshwater species21

(Adapted from Richardson, 1905)

21. (24) Mandibles with a palp. Lateral margin of head not cleft.22
22. (23) Flagella of first antennae (the shorter) average 14 articles. No lobe on head behind eyes. *Asellus communis* Say.
23. (22) Flagella of first antennae average 9 articles. Small lateral lobes at base of head just behind eyes (Fig. 1). *Asellus intermedius* Forbes.
24. (21) Mandibles without a palp. Lateral margins of head with a deep conspicuous cleft (Fig. 3).....25
25. (26) Uropods as long as terminal segment of body. *Mancasellus danielsi* Richardson.
26. (25) Uropods shorter than terminal segment of body27
27. (28) Propodus (second segment from distal end) of first pair of legs with a triangular process. Sides of cleft on lateral margins of head not meeting (Fig. 3). *Mancasellus tenax* (Smith).
28. (27) Propodus of first pair of legs with three acute teeth. Sides of cleft on lateral margins of head sometimes meeting. *Mancasellus dilatus* (Smith).

DISTRIBUTION OF THE SPECIES

Although the data available on the various species of isopods as they are now known to occur in Michigan are incomplete, certain general statements on the dispersal of these crustaceans within the state can be made at this time. Since each of the terrestrial species has different habitat requirements, their distribution will be discussed from this point of view. Locations of townships from which isopods of the various species have been collected are shown by symbols on the accompanying maps (Figs. 15-18). In many instances a single symbol may stand for several records for a particular species from a township. Check lists for the majority of the species have also been included in order to give more exact information on distribution. These lists (Tables 1-9) include all known records previously published by others, as well as records based on specimens taken during the present investigation, and those unpublished records from the collections of the University of Michigan Museum of Zoology. Where the records are not mine, the references for them are given, while those based on the collections of the University of Michigan Museum of Zoology are indicated by UMMZ.

TERRESTRIAL SPECIES

Ligidium longicaudatum Stoller

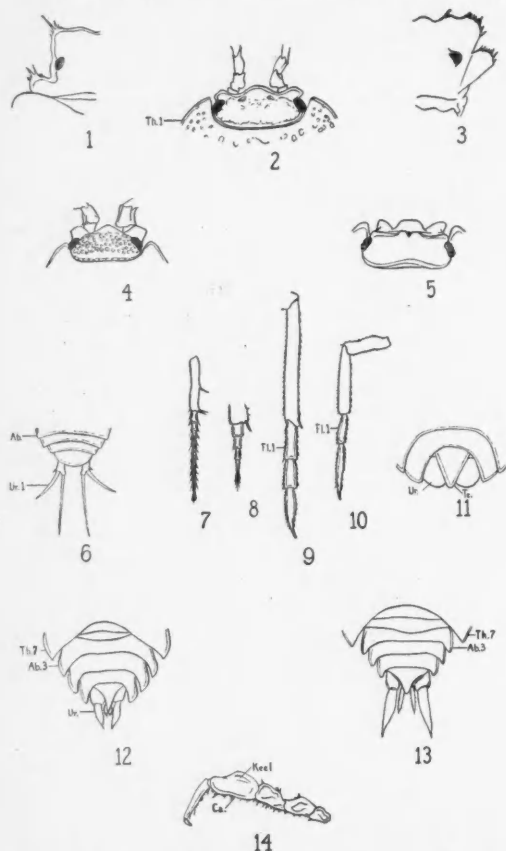
As previously stated, *Ligidium longicaudatum* is probably one of the few native terrestrial isopods of North America. Although not extensively collected in Michigan (Fig. 15), all specimens were taken in situations that were protected from flooding, but still always wet. Walker (1927) states that such conditions are essential in its habitat. In Michigan, it has been found only in three southern counties, Berrien, Washtenaw, and Wayne. However, during this investigation very few areas, where the proper conditions existed for the species, were examined. In the University of Michigan Museum of Zoology there are specimens collected under leaves in a wet woodland of Redford Township, Wayne

County. There is a specimen in the United States National Museum collected at Lakeside, Berrien County, but its habitat is not known. Pearse (1910) reported finding this species near the "Overflow," Ann Arbor, Washtenaw County. During the present investigation it was found in abundance among moss in marshlands east of Ann Arbor (T2S-R6E-S36). During the winter of 1940, in this locality,

Ligidium longicaudatum was very active among the ice crystals under the moss, although the area had been frozen for more than a month.

Trichoniscus demivirgo Blake

One of the least known terrestrial isopods of this continent is *Trichoniscus demivirgo*. Inasmuch as it averages only three millimeters in length, it is the smallest of the Michigan species. Its small size and agility may be the chief reasons why it has not been collected as frequently as the other terrestrial isopods. This species occurs in widely scattered areas in the northern part of the United States: from New England (Norton 1909, Blake 1931) as far west as Seattle, Washington (Dailey & Hatchett 1940). However, it has not been previously reported for Michigan. In this state it has been found in two localities in the area around Ann Arbor. Both situations were wet spots in open deciduous woods. This isopod was abundant there under stones and



FIGS. 1-14. Some distinguishing features of various isopods. Fig. 1—Head of *Asellus intermedius* Forbes; Fig. 2—Head of *Tracheoniscus rathkei* (Brandt); Fig. 3—Head of *Mancasellus tenax* (Smith); Fig. 4—Head of *Porcellio scaber* Latreille; Fig. 5—Head of *Armadillidium nasatum* Budde-Lund; Fig. 6—Last abdominal segments and uropods of *Ligidium longicaudatum* Stoller; Fig. 7—Flagellum of second antenna of *Ligidium longicaudatum* Stoller; Fig. 8—Flagellum of second antenna of *Trichoniscus demivirgo* Blake; Fig. 9—Flagellum of second antenna of *Oniscus asellus* Linnaeus; Fig. 10—Flagellum of second antenna of *Cylisticus conveys* (De Geer); Fig. 11—Last abdominal segments and uropods of *Armadillidium nasatum* Budde-Lund; Fig. 12—Posterior portion of *Oniscus asellus* Linnaeus; Fig. 13—Posterior portion of *Porcellionides pruinosus* (Brandt); Fig. 14—Seventh leg of male *Tracheoniscus rathkei* (Brandt). Key to abbreviations: Ab.—Abdomen (number refers to specific segment), Ca.—Carpus, FL. 1—First article of antenna, Th.—Thorax (numbers refer to specific segments), Te.—Telson, Ur. and Ur. 1—outer branch (expodite) of uropods.



FIG. 15. Distribution within the counties of Michigan of *Ligidium longicaudatum* Stoller, *Oniscus asellus* Linnaeus, *Porcellio scaber* Latreille and *Porcellio spinicornis* Say. Key to abbreviations of county names: Ale.—Alcona; Al.—Alger; All.—Allegan; Alp.—Alpena; Ant.—Antrim; Are.—Arenac; Bar.—Baraga; Barry.—Barry; Bay.—Bay; Ben.—Benzie; Ber.—Berrien; Bra.—Branch; Cal.—Calhoun; Cass.—Cass; Cha.—Charlevoix; Che.—Cheboygan; Chi.—Chippewa; Clare.—Clare; Cli.—Clinton; Cra.—Crawford; Del.—Delta; Dic.—Dickinson; Eaton.—Eaton; Em.—Emmet; Gen.—Genesee; Gla.—Gladwin; Gog.—Gogebie; Gr.—Grand Traverse; Gra.—Gratiot; Hill.—Hillsdale; Ho.—Houghton; Huron.—Huron; Ing.—Ingham; Ionia.—Ionia; Ios.—Iosco; Iron.—Iron; Isa.—Isabella; Jac.—Jackson; Kam.—Kalamazoo; Kal.—Kalkaska; Kent.—Kent; Kew.—Keweenaw; Lake.—Lake; Lap.—Lapeer; Le.—Leelanau; Len.—Lenawee; Liv.—Livingston; Luce.—Luce; Mac.—Mackinac; Mab.—Macomb; Man.—Manistee; Mar.—Marquette; Mas.—Mason; Mec.—Mecosta; Men.—Menominee; Mid.—Midland; Mis.—Missaukee; Mor.—Monroe; Moe.—Montcalm; Mon.—Montmorency; Mus.—Muskegon; New.—Newaygo; Oak.—Oakland; Oee.—Oceana; Oge.—Ogemaw; Ont.—Ontonagon; Ose.—Oseola; Osc.—Oscoda; Ots.—Otsego; Ott.—Ottawa; Pre.—Presque Isle; Ros.—Roscommon; Sag.—Saginaw; St. C.—Saint Clair; St. J.—Saint Joseph; San.—Sanilac; Sch.—Schoolcraft; Shi.—Shiawassee; Tus.—Tuscola; Van.—Van Buren; Was.—Washtenaw; Way.—Wayne; Wex.—Wexford.

decaying leaves. These situations agree rather closely with the description of the habitat by Blake (1931).

Oniscus asellus Linnaeus

Although it has been recorded from the provinces of Ontario and Quebec, Canada (Walker, 1927) and as far west as Rock Island, Illinois (Richardson, 1905), *Oniscus asellus* has not been reported previously from Michigan. In this state it has been collected from widely scattered areas: Ann Arbor, Washtenaw County; Bay City, Bay County; and on Mackinac and Bois Blanc Islands in the Straits of Mackinac (Fig. 15). This isopod was abundant in these localities, all of which were around human settlements. It was found in protected situations which varied from moist to wet.

Porcellio scaber Latreille

This species, which has a rather extensive range in North America, is widespread throughout most of the lower peninsula of Michigan (Fig. 15; Table 1). It has been collected from the southernmost tier of counties to the Straits of Mackinac, and Hatch (1939) reports it from Houghton County in the upper peninsula. Blake (1931a) states that *P. scaber* is a hygrophilous species in New England. To a certain degree, this is also true in Michigan. During the present investigation, it was found along the shores of lakes and rivers (Table 1). Usually, in such habitats, it occurred under logs, boards, straw or drift material. It was more abundant on the outer beaches of lakes than in the other regions along the shores. This is in contrast to *Cylisticus converus*, which apparently prefers the middle beach.

TABLE 1. Michigan Records of *Porcellio scaber* Latreille.

COUNTY	LOCALITY	LOCUS KEY	REFERENCE
Bay	Bay City	T14N-R5E	
Benzie	Shore Platte Lake	T27N-R15W-S36	
Branch	Shore Coldwater Lake	T7S-R6W-S35	
"	Shore Morrison Lake	T5S-R6W-S32	
Charlevoix	Hog Isl., L. Michigan	----	
"	Pismyre Isl., L. Mich.	----	
Cheboygan	Shore Munro Lake	T37N-R3W-S9	
"	Farm—Hebron Twp.	T38N-R3W-S31	
Clare	Shore Shingle Lake	T18N-R5W-S8	
Eaton	Shore Pine Lake	T1N-R5W-S31	
Emmet	Shore Lake Michigan	T38N-R6W-S34	
Gladwin	Gladwin St. Park	T18N-R2W-S1	
Houghton (UP)	Calumet		Hatch '39
Huron	Harbor Beach	T16N-R15E-S12	
Ingham	Lansing	T4N-R2W	
"	Williamston	T4N-R1E-S36	
Lapeer	Shore Lake Pleasant	T7N-R1E-S4	
Leelanau	Shore Glen Lake	T29N-R14W-S29	
Lenawee	Banks Raisin River	T7S-R4E-S22	
Muskegon	Shore White Lake	T12N-R17W-S33	
Oakland	Shore Lake Orion	T5N-R10E	
Saginaw			Richardson '05
Sanilac	Lexington Twp. L. Huron	T10N-R16E-S13	
Washtenaw	Ann Arbor		Pearse '10
"	Arboretum—Ann Arbor	T2S-R6E-S28	
"	Basement—Ann Arbor	T2S-R6E-S33	
"	Island Park—Ann Arbor	T2S-R6E-S21	

Porcellio scaber, in other parts of the country, has usually been recorded from the vicinity of human settlements (Blake 1931a, Van Name 1936). Not only does it occur within cities and around farms in Michigan, but also in areas devoid of habitations. It has been collected in several cities in Michigan. This isopod also was found in a beech-maple forest some distance from human habitations. There are specimens of *P. scaber* in my collections that were taken from a group of small islands (Pismyre, Hog and Hat) located in Lake Michigan. *Cylisticus converus* was the only other isopod that occurred on these islands. It is of interest that *P. scaber* was not taken on Mackinac Island, where most of the other terrestrial species were collected.

Porcellio spinicornis Say

According to Van Name (1936) *Porcellio spinicornis* has become established in northeastern North America, where it probably was introduced from Europe. Although a subspecies, *occidentalis*, the identity of which is questioned by Van Name (1940), is found on the Pacific Coast (Miller 1936), *P. spinicornis* has not been reported farther west than Michigan. The northernmost record for the state—Eagle Harbor, Keweenaw County (Hatch 1939)—is nearly at the northern boundary of the species' range as delimited by the Canadian records of Johansen (1926) and Walker (1927).

In the lower peninsula of Michigan it has been found to be widely scattered in its occurrence (Fig. 15, Table 2). It has been collected in eight counties of the lower peninsula, but only from limited areas in each of them. Usually just a few specimens were seen in a single locality. One exception to this occurred during the spring of 1942, when large aggregations were found on a rocky beach of Crystal Lake, Montcalm County. Just previous to the visit to this locality, a great many mayflies had emerged from the lake, and their exuviae had been cast up on the shores in windrows. *P. spinicornis* was found feeding in these piles of exuviae. It was the only isopod present, although not far away *Cylisticus converus* and *Tracheoniscus rathkei* were collected.

This species of *Porcellio* apparently is rather restricted in its choice of habitats. Stoller (1902) states that it "seems to prefer the crevices of rocks, specially shady limestone ledges." These also are the situations where this species has been taken most frequently during the present investigation. On Mackinac Island, individual specimens were seen crawling over shaded limestone outcroppings. It has been found on the shores of several lakes (Table 2), where the beaches were composed of either sandy marl or stones.

P. spinicornis has been collected in places usually not considered desirable situations for isopods. It has been taken in the attics of two abandoned farm houses, one in Cheboygan County and the other in Washtenaw County. That these were not accidental records is illustrated by the fact that during three consecutive summers—1940, 1941, 1942—specimens

of this species were collected in the farmhouse in Cheboygan County. Both of these houses were good collecting places for pseudoscorpions which generally prefer a dry situation. In these instances just mentioned, the isopods were found under pieces of fallen plaster, particles of which they may have been ingesting. Many isopods raised in the laboratory in plaster cups have been seen gnawing on the sides of the container. *P. spinicornis* was once taken from a concrete window sill on the third story of the Natural Science Building on the campus of the University of Michigan. It has also been collected along the walls of basements and in a store in Ann Arbor. This peculiar preference for habitats where lime is available may account for the rather spotted occurrence of the species.

TABLE 2. Michigan Records of *Porcellio spinicornis* Say.

COUNTY	LOCALITY	LOCUS KEY	REFERENCE
Bay	Bay City	T14N-R5E	Hatch '39
Cheboygan	Old house, Munro Lake	T37N-R3W-S16	
Keweenaw (UP)	Eagle Harbor		
Lenawee	Shore Devil's Lake	T5S-R1E-S27	
Mackinac (UP)	Mackinac Island	----	
Montcalm	Shore Crystal Lake	T10N-R5W-S9	
Oakland	Shore Deer Lake	T4N-R9E-S30	
Sanilac	Lexington Twp., L. Mich.	T10N-R16E-S13	
Washtenaw	Arboretum—Ann Arbor	T2S-R6E-S28	
"	U. of M. Campus— Ann Arbor	T2S-R6E-S29	
"	Basement—Ann Arbor	T2S-R6E-S33	
"	Island Park—Ann Arbor	T2S-R6E-S21	
"	Deserted House	T2S-R5E-S21	
"	Shore North Lake	T1S-R4E-S18	

Porcellionides pruinosus (Brandt)

From the available data on the distribution of this species in Michigan, it appears to be limited to the southern part of the state (Fig. 16, Table 3). In the northern part of the continent, it has been reported only from southern Ontario, Canada (Walker 1927) and from Massachusetts (Richardson 1905, Blake 1931a). From these northernmost records, it appears that the range of *P. pruinosus* in Michigan may extend somewhat farther north than is apparent from the present records. However, Michigan, north of the localities from which this species was taken, is not as thickly settled as in the southern part. This, then, may partially account for the limited range of *Porcellionides pruinosus* in the state. Hatch (1939) reports it from Detroit, and all of my records are for specimens taken within cities or in highly agricultural areas.

Cylisticus convexus (De Geer)

In the extent of its distribution in Michigan, this species is second only to *Tracheoniscus rathkei*. It is distributed throughout most of the lower peninsula, and has been collected in the Keweenaw Peninsula and Isle Royale of northern Michigan (Fig. 16). In the majority of localities, this species was very nu-



FIG. 16. Distribution within the counties of Michigan of *Armadillidium nasatum* Budde-Lund, *Armadillidium vulgare* (Latreille), *Cylisticus convexus* (De Geer) and *Porcellionides pruinosus* (Brandt). (For key to abbreviations of county names, see explanation of Fig. 15.)

TABLE 3. Michigan Records of *Porcellionides pruinosus* (Brandt).

COUNTY	LOCALITY	LOCUS KEY	REFERENCE
Eaton	Shore Pine Lake	T1N-R5W-S31	Hatch '39
Ingham	Williamston	T4N-R1E-S36	
Monroe	Banks Raisin River	T6S-R7E-S14	
"	Toledo Beach, L. Erie	T7S-R9E-S31	
Washtenaw	Arboretum—Ann Arbor	T2S-R6E-S28	
Wayne	Detroit		

merous. Table 4 lists the records of this species from Michigan, and also indicates that it was taken in many of the townships in Washtenaw and Cheboygan Counties where intensive collections were made. Therefore, further data would probably show this species to be even more abundant than is evident from the present information.

Cylisticus convexus has been collected in many different types of habitats. It was particularly abundant on most of the rocky beaches where collections were made. It has also been taken on other types of beaches as well as along river banks, when drift and other debris were present, but seldom was it as plentiful as on the rocky shores. When found along lakes, this species was more abundant in the region of the middle beach than on either the inner or outer beaches, where usually only scattered individuals were to be found. In Michigan, *C. convexus* was very abundant on several small islands in Lake Michigan belonging to Charlevoix County. These islands are principally gull and tern rookeries some distance from the mainland. Only this species and *Porcellio scaber* were collected there during the summers of 1940 and 1941. *C. convexus* has been

taken from limestone outcroppings and quarries in the northern part of the lower peninsula. Occasionally in Michigan it has been found along the margins of mixed deciduous woods. It was not abundant in the last situation. Never was it collected in central portions of woodlands, unless roads or other man-made clearings were present. This species, like many of the other terrestrial isopods, is to be found in large numbers within cities. It is the predomi-

nant species on Mackinac Island, which was among the first places in Michigan to be settled. In general, *Cylisticus convexus* prefers a more moist situation than do the species of *Armadillidium*, *Porcellio* and *Tracheoniscus*. This is illustrated by the fact that it is very abundant in such moist situations as rocky beaches and along river banks, where it may be the predominant isopod, while on the other hand, in drier conditions, such as are found in cities and woodlands, it is scattered and is not an abundant species.

TABLE 4. Michigan Records of *Cylisticus convexus* (De Geer).

COUNTY	LOCALITY	LOCUS KEY	REFERENCE
Antrim	Woodland, Elk Rapid Twp.	T29N-R9W-S29	
Barry	Shore Gun Lake	T2N-R10W-S5	
Branch	Shore Coldwater Lake	T7S-R6W-S35	
Calhoun	Park—Lee Twp.	T1S-R5W-S7	
Charlevoix	Shore L. Charlevoix	T3N-R7W-S15	
"	Hat Isl., L. Michigan	----	
"	Hog Isl., L. Michigan	----	
"	Pismyre Isl., L. Mich.	----	
Cheboygan	Shore Douglas Lake	T37N-R3W-S33	
"	Shore Burt Lake	T36N-R3W-S8	
"	Banks of Mill Creek	T39N-R3W-PC334	
"	Campbell Quarry	T35N-R2W-S36	
"	Banks Sturgeon River	T33N-R2W-S7	
"	Aloha State Park	T36N-R1W-S8	
"	Shore Long Lake	T36N-R1W-S12	
Eaton	Shore Pine Lake	T1N-R5W-S31	
Emmet	Shore Lake Michigan	T38N-R6W-S34	
"	Shore Straits Mackinac	T39N-R4W-S11	
Genesee	Flint		
Gladwin	Gladwin State Park	T18N-R2W-S1	
Houghton (UP)	Calumet		Hatch '39
Huron	Harbor Beach	T16N-R15E-S12	
"	Owendale	T15N-R10E-S15	
Ingham	Lansing	T4N-R2W	
Kalamazoo	Woods W. of Schoolcraft	T4S-R12W-S13	
Keweenaw (UP)	Eagle Harbor		Hatch '39
"	Ile Royale		Adams '09
Leelanau	Shore Glen Lake	T29N-R14W-S29	
Lenawee	Shore Devil's Lake	T5S-R1E-S27	
"	Banks Wolf Creek	T6S-R3E-S31	
"	Banks Raisin River	T7S-R4E-S22	
Mackinac (UP)	Mackinac Island	----	
"	Bois Blanc Island	----	
Macomb	Banks Clinton River	T2N-R14E	
Manistee	Orchard Beach St. Park	T22N-R17W-S25	
Monroe	Banks Raisin River	T6S-R7E-S14	
"	Toledo Beach, L. Erie	T7S-R9E-S31	
Montcalm	Shore Crystal Lake	T10N-R5W-S9	
Mostmorency	Banks Thunder Bay River	T31N-R4E-S23	
Muskegon	Shore White Lake	T12N-R17W-S33	
Oakland	Shore Lake Orion	T5N-R10E	
Presque Isle	Shore Grand Lake	T33N-R8E-S8	
"	Shore Black Lake	T35N-R2E-S8	
Saginaw	Saginaw		Richardson '05
Sanilac	Lexington Twp. L. Huron	T10N-R16E-S13	
"	Delaware Twp. L. Huron	T14N-R16E-S32	
Washtenaw	Ann Arbor		Pearse '10
"	Ann Arbor		Hatch '39
"	Arboretum—Ann Arbor	T2S-R6E-S28	
"	Island Park—Ann Arbor	T2S-R6E-S21	
"	Basement—Ann Arbor	T2S-R6E-S33	
"	White's Woods	T2S-R6E-S30	
"	Shore Sugar Lake	T2S-R3E-S32	
"	Field on Chelsea Road	T1S-R3E-S22	
Wayne	Detroit		Hatch '39

Tracheoniscus rathkei (Brandt)

Tracheoniscus rathkei, which is widely distributed in eastern United States (Van Name 1936), is to be found throughout all of the lower peninsula of Michigan (Fig. 17). It has also been collected in the eastern part of the upper peninsula—Chippewa, Luce and Mackinac Counties. There are no records from the remaining counties in that part of the state. For the lower peninsula, however, there are records of this species for every county (Table 5). *T. rathkei* is the predominant terrestrial isopod of the region. It occurs in great abundance in most parts of southern Michigan. There is only one region of the lower peninsula in which this species is not abundant—the jack pine belt that stretches across the north-central area of the peninsula. In this region it is usually the only terrestrial isopod to be found (Figs. 17 & 19). However, *Cylisticus convexus* and *Porcellio scaber* may occasionally occur along water courses or in towns of this zone. In contrast to *Porcellio spinicornis*, *T. rathkei* does not appear to be specific in its habitat preferences. This adaptability to various conditions may account for its wide distribution and abundance in the state.

Habitats for this species cited by Richardson (1905) are "woodsheds, greenhouses, on rotten logs, under bricks and boards, under logs, at river bot-



FIG. 17. Distribution within the counties of Michigan of *Tracheoniscus rathkei* (Brandt). (For key to abbreviations of county names, see explanation to Fig. 15.)

TABLE 5. Michigan Records of *Tracheoniscus rathkei* (Brandt).

COUNTY	LOCALITY	LOCUS KEY	REFERENCE
Alcona	Harrisville		UMMZ
"	Woodland S. of Glennie	T25N-R6E	
"	Pasture E. of Curran	T28N-R5E	
Allegan	Woodland N. of Wayland	T4N-R11W-S31	
"	Field W. of Dorr	T4N-R12W-S16	
"	Field E. of Overisel	T4N-R14W-S13	
Alpena	Woodland, Alpena Twp.	T32N-R8E-S27	
Antrim	Woodland, Elk Rapids Twp.	T29N-R9W-S29	
"	Pasture N. of Mud Lake	T30N-R9W-S24	
Arenac	Maple woods, Standish Twp.	T18N-R4E-S35	
"	Woodland, Au Gres Twp.	T19N-R6E-S16	
"	Shore Lake Huron	T20N-R7E-S12	
Barry	Shore Gun Lake	T2N-R10W-S5	
"	Woodland, Woodland Twp.	T4N-R7W-S12	
Bay	Bay City	T14N-R5E	
"	Woodland N. of Kawkawlin	T15N-R4E-S35	
Benzie	Woodland E. of Honor	T26N-R14W-S9	
"	Shore Platte Lake	T27N-R15W-S36	
Berrien	Pasture near St. Joseph R.	T8S-R18W-S4	
"	Shore Lake Michigan	T3S-R18W-S11	
Branch	Shore Coldwater Lake	T7S-R6W-S35	
"	Banks Prairie River	T7S-R8W-S25	
Calhoun	Park—Lee Twp.	T1S-R5W-S31	
"	Pasture, Battle Creek Twp.	T2S-R8W-S17	
Cass	Woodland, Marcellus Twp.	T5S-R13W-S13	
"	Banks Dowagiac Creek	T5S-R16W-S35	
Charlevoix	Pasture, Norwood Twp.	T33N-R8W-S24	
"	Shore Lake Charlevoix	T33N-R7W-S15	
Cheboygan	Burt Lake		Hatch '39
"	Shore Burt Lake	T36N-R3W-S8	
"	Shore Burt Lake	T36N-R3W-S17	
"	Shore Douglas Lake	T37N-R3W-S28	
"	Shore Douglas Lake	T37N-R3W-S17	
"	Shore Munro Lake	T37N-R3W-S9	
"	Indian River St. Park	T35N-R3W-S25	
"	Banks Mill Creek	T29N-R3W-PC334	
"	Shore Silver Lake	T33N-R3W-S11	
"	Campbell Quarry	T35N-R2W-S36	
"	Woodland, Pigeon River	T34N-R2W-S2	
"	Woodland E. of Wolverine	T33N-R2W-S8	
"	Aloha State Park	T36N-R1W-S8	
"	Shore Long Lake	T36N-R1W-S12	
"	Banks Milliken Creek	T34N-R1W-S3	
"	Banks Milliken Creek	T34N-R1W-S14	
"	Pigeon River St. Forest	T34N-R1W-S32	
"	Banks Black River	T34N-R1E-S11	
"	Banks Nigger Creek	T36N-R2W-S16	
"	Dried Bog, Hebron Twp.	T38N-R3W-S31	
Chippewa (UP)	Shore Lake Superior	T48N-R7W-S15	
Clare	Pasture, Arthur Twp.	T18N-R3W-S2	
"	Pasture, Hutton Twp.	T18N-R4W-S25	
"	Shore Shingle Lake	T18N-R5W-S8	
Clinton	Maple Woods, Ovid Twp.	T7N-R1W-S6	
"	Hardwoods, Riley Twp.	T6N-R3W-S8	
"	Pasture, Watertown Twp.	T5N-R3W-S1	
Crawford	Banks Au Sable River	T26N-R1W-S29	
"	Shore Lake Margrethe	T26N-R4W-S10	
Eaton	Woods S. of Grand Ledge	T3N-R4W-S2	
"	Banks Battle Creek	T2N-R4W-S19	
"	Shore Pine Lake	T1N-R5W-S31	
Emmet	Shore Lake Michigan	T39N-R6W-S34	
"	Shore Straits of Mackinac	T39N-R4W-S11	
"	Shore Straits of Mackinac	T39N-R4W-S28	
"	Shore Carp Lake	T39N-R4W-S15	
"	Shore Carp Lake	T38N-R4W-S24	
Genesee	Flushing State Park	T8N-R5E-S27	
Gladwin	Shore Wixon Lake	T17N-R1W-S36	
"	Gladwin State Park	T18N-R2W-S1	

TABLE 5. Michigan Records of *Tracheoniscus rathkei* (Brandt)—(Continued).

COUNTY	LOCALITY	LOCUS KEY	REFERENCE
Grand Traverse	Woodland, Paradise Twp.	T25N-R10W-S1	
"	Woodland, Blair Twp.	T26N-R11W-S20	
Gratiot	Woodland E. of Newark	T10N-R3W-S14	
Hillsdale	Hardwoods, Hillsdale Rd.	T7S-R3W-S23	
"	Pasture, Edon Road	T8S-R4W-S2	
Huron	Farm, McKinley Twp.	T17N-R10E-S28	
"	Owendale	T15N-R10E-S15	
"	Swamp, Sand Beach Twp.	T16N-R15E-S1	
"	Shore Lake Huron	T18N-R14E-S2	
Ingham	Field, Leroy Twp.	T3N-R2E-S4	
"	Field, Howell Road	T3N-R1W-S34	
"	Pasture, Onondago Road	T2N-R2W-S9	
"	Banks Grand River	T1N-R2W-S28	
"	Near House, Lansing	T4N-R2W	
"	Near House, Williamston	T4N-R1E-S36	
Ionia	Woodland S. of Belding	T8N-R8W-S23	
"	Hardwoods N. of Saranac	T6N-R8W-S1	
"	Shore Morrison Lake	T6N-R8W-S36	
Iosco	Creek Bed, Alabaster Twp.	T21N-R7E-S14	
Isabella	Pasture, Broomfield Twp.	T14N-R6W-S23	
"	Banks Chippewa River	T14N-R5W-S17	
Jackson	Banks Grand River	T1S-R1W-S35	
"	Vineyard Lake St. Park	T4S-R2E-S28	
Kalamazoo	Woodland near Indian L.	T4S-R10W-S9	
"	Farmland, Comstock Twp.	T2S-R10W-S6	
"	Woodland, Prairie Twp.	T4S-R12W-S13	
Kalkaska	Field, Kalkaska	T27N-R7W-S17	
Kent	Pasture, Walker Twp.	T7N-R12W-S2	
"	Woodland, Alpine Twp.	T8N-R12W-S12	
Lake	Manistee National Forest	T17N-R11W-S6	
Lapeer	Woodland on US53	T7N-R12E-S29	
"	Shore Lake Pleasant	T7N-R11E-S4	
"	Shore Lake Nepessing	T7N-R9E-S23	
Leelanau	Shore Glen Lake	T29N-R14W-S29	
"	Pasture, Solon Twp.	T28N-R12W-S8	
Lenawee	Shore Evans Lake	T6S-R3E-S6	
"	Banks Raisin River	T7S-R4E-S22	
"	Field along Wolf Creek	T6S-R3E-S31	
"	Shore Devil's Lake	T5S-R1E-S27	
"	Shore Iron Lake	T8S-R2E-S2	
Livingston	Woodland near Hartland		UMMZ
"	Shore Strawberry Lake	T1N-R5E-S27	
"	Shore Brighton Lake	T2N-R5E-S36	
"	Field along Cedar River	T4N-R3E-S32	
"	Banks Huron River	T1N-R5E-S24	
Luce (UP)	Soo Junction	T46N-R8W-S35	
Mackinac (UP)	Mackinac Island	- - -	
"	Bois Blanc Island	- - -	
"	Swamp along Paquin Creek	T43N-R7W-S34	
Macomb	Shore Lake St. Clair	T1N-R13E	
"	Banks Clinton River	T2N-R13E	
Manistee	Shore Bar Lake	T24N-R16W-S15	
"	Orchard Beach St. Park	T22N-R17W-S25	
"	Shore Portage Lake	T23N-R16W-S36	
"	Banks Cedar Creek	T23N-R13W-S5	
Mason	Shore Emerson Lake	T18N-R15W-S15	
"	Woodland Custer Twp.	T18N-R16W-S14	
Mecosta	Woodland near Big Rapids		UMMZ
"	Banks Muskegon River	T14N-R10W-S20	
"	Shore Section Lake	T14N-R8W-S16, 21	
Midland	Banks Chippewa River	T14N-R2W-S8	
"	Woodland, Homer Twp.	T14N-R1E-S16	
Missaukee	Lake Missaukee St. Park	T22N-R8W-S1	
"	Pasture, Reeder Twp.	T22N-R7W-S1	
"	Banks Muskegon River	T23N-R5W-S35	
Monroe	Banks Raisin River	T6S-R7E-S11	
"	Toledo Beach, L. Erie	T7S-R9E-S31	
"	Woodland, Bullock School	T8S-R7E-S9	
Montcalm	Woodland E. of Crystal	T10N-R5W-S15	
"	Shore Crystal Lake	T10N-R5W-S9	

TABLE 5. Michigan Records of *Tracheoniscus rathkei* (Brandt)—(Continued).

COUNTY	LOCALITY	LOCUS KEY	REFERENCE
Montcalm	Pasture	T10N-R6W-S21	
Montmorency	Pasture	T32N-R4E-S24	
"	Banks Thunder Bay River	T31N-R4E-S23	
"	Woodland along Smith Creek	T30N-R3E-S7	
"	Banks Hay Meadow Creek	T30N-R2E-S11	
Muskegon	Woodland W. of Casnovia	T10N-R13W-S19	
"	Shore White Lake	T12N-R17W-S33	
Newaygo	Woodland E. of Hesperia	T14N-R14W-S32	
"	Banks White River	T14N-R13W-S30	
Oakland	Sylvan Lake		Hatch '39
"	Fenton		UMMZ
"	Woodland near Co. Line		UMMZ
"	Woodland E. of South Lyon		UMMZ
"	Shore Deer Lake	T4N-R9E-S30	
"	Park, Southfield Twp.	T1N-R10E-S8	
Oceana	Pasture, Newfield Twp.	T14N-R15W-S32	
Ogemaw	Banks Rifle River	T22N-R3E-S21	
"	Banks Nester Creek	T22N-R4E-S22	
Oscoda	Woodland, Oscoda Twp.	T18N-R8W-S36	
"	Banks McKinstry Creek	T17N-R9W-S19	
Oscoda	Pasture, Big Creek Twp.	T26N-R2E-S19	
Otsego	Shore Cogswell Lake	T31N-R3W-S35,36	
Ottawa	Woodland N. of Holland	T6N-R15W-S32	
"	Woodland, Springlake	T8N-R16W-S24	
"	Woodland, Wright Twp.	T8N-R13W-S34	
Presque Isle	Shore Grand Lake	T33N-R8E-S8	
"	Shore Lake Huron	T37N-R2E-S14	
"	Shore Little Lake	T35N-R6E-S30	
"	Shore Ocqueoc Lake	T36N-R3E-S30	
"	Farmland E. of Onaway	T34N-R3E-S6	
"	Field S. E. of Millersberg	T34N-R3E-S25	
"	Pasture S. of Hawks	T33N-R4E-S12	
Roscommon	Shore Houghton Lake	T22N-R4W-S3	
"	Field, Roscommon Twp.	T23N-R4W-S33	
"	Woodland, Richfield Twp.	T23N-R1W-S7	
Saginaw	Saginaw		Richardson '05
"	Creek banks, Albee Twp.	T10N-R4E-S34	
"	Banks Shiawassee River	T10N-R3E-S22	
"	Dump E. of Brant	T10N-R2E-S17	
Sanilac	Shore Lake Huron	T14N-R16E-S32,18	
Shiawassee	Woodland, Bancroft Road	T5N-R3E-S11	
"	Banks Shiawassee River	T6N-R3E-S14	
St. Clair	Banks Belle River	T5N-R16E-S32	
St. Joseph	Shore Klinger Lake	T8S-R11W-S2	
"	Banks St. Joseph River	T5S-R9W-S32	
"	Woodland, Flowerfield Twp.		
Tuscola	Woodland along US 23	T5S-R12W-S27	
Van Buren	Pasture, Geneva Twp.	T14N-R8E-S3	
"	Woodland N. of Gobles	T1S-R16W-S12	
Washtenaw	Ann Arbor	T1S-R13W-S18	
"	Ann Arbor		Pearse '10
"	Woodland on Geddes Road		Hatch '39
"	Woodland, Joy & Pontiac Rds.		UMMZ
"	Superior Twp.		UMMZ
"	Arboretum—Ann Arbor	T2S-R6E-S28	
"	Saginaw Forest	T2S-R5E-S25	
"	White's Woods	T2S-R6E-S30	
"	Dexter—Huron Park	T2S-R5E-S5	
"	Shore Cavanaugh Lake	T2S-R3E-S8	
"	Shore Sugar Loaf Lake	T2S-R3E-S32	
"	Loch Alpine Park	T2S-R5E-S3	
"	Swamp along Zeeb Road	T2S-R5E-S27	
"	Pasture along Sylvan Road		
"	Pasture along Dancer Road	T3S-R5E-S3	
"	Shore North Lake	T3S-R4E-S26	
"		T1S-R4E-S18	

TABLE 5. Michigan Records of *Tracheoniscus rathkei* (Brandt)—(Continued).

COUNTY	LOCALITY	LOCUS KEY	REFERENCE
Washtenaw	Field along Chelsea Road	T1S-R3E-S22	
Wayne	Redford Golf Course		UMMZ
"	Huron River Park	T4S-R9E-S27	
Wexford	Banks Manistee River	T23N-R12W-S11	
"	Banks Soper Creek	T23N-R10W-S5	

tom." For Michigan, at least, several more situations should be added. It is abundant in cities, but is not, as Van Name (1936) implies, to be found primarily around human settlements. More than any other species, *Tracheoniscus rathkei* is to be found in the woods. Very few deciduous woods that were investigated in the lower peninsula failed to yield at least one specimen of this species. On the few occasions when it was not collected, the woods were usually so dense that the forest floor was almost devoid of animal life, or the situation was much too dry. This species is the only isopod that has been collected in the aspen woods of Michigan, and in these few instances it was not particularly numerous. Dryness of the forest floor may be one reason why isopods are usually not to be found in aspen associations. *T. rathkei* occurred in temporary pools that had dried up in early summer, although it might be the only terrestrial animal, with the possible exception of land snails, which had invaded the area. Of primary importance among the specific woodland habitats frequented by this species are rotting logs and stumps. From late fall through winter to spring, decaying logs seem to be preferred to other situations, since large aggregations have been found there when the species could not be collected elsewhere in the region. *Tracheoniscus rathkei*, although typically a woodland species, nevertheless also frequents lake shores, pastures, grasslands, and cleared areas along roadsides.

Armadillidium vulgare (Latreille)

This isopod has been collected in widely scattered areas in the lower peninsula of Michigan (Fig. 16; Table 6). The northernmost records reported by others are Salem, Massachusetts (Blake 1931a), Toronto, Canada (Walker 1927) and Seattle, Washington (Hatch 1939). In Canada, it is principally found in greenhouses (Walker 1927). During the summer of 1942 several specimens were collected along the beach of Fairy Island, Douglas Lake, Cheboygan County. This locality is farther north than the first two records cited above, and has a more rigorous climate than Seattle. The area where the collection was made had been intensively searched during the three preceding summers and during these periods *A. vulgare* had not been collected there. It is my opinion, therefore, that the lack of previous records from this locality can be explained only by assuming that this species had been introduced into the region during the spring or early summer of 1942, when plantings of decorative shrubs, not in-

TABLE 6. Michigan Records of *Armadillidium vulgare* (Latreille).

COUNTY	LOCALITY	LOCUS KEY	REFERENCE
Bay	Near dwelling, Bay City	T14N-R5E	
Branch	Beach, Coldwater Lake	T7S-R6W-S35	
Cass	Banks, Dowagiac Creek	T5S-R16W-S35	
Cheboygan	Fairy Island, Douglas L.	T37N-R3W-S30	
Ingham	Near dwelling, Lansing	T4N-R2W	
Monroe	Toledo Beach on L. Erie	T7S-R9E-S31	
Washtenaw	Ann Arbor		Hatch '39
"	Arboretum—Ann Arbor	T2S-R6E-S28	
"	Basement—Ann Arbor	T2S-R6E-S33	
"	Bot. Garden—Ann Arbor	T2S-R6E-S31	
"	U. of M. campus—Ann Arbor	T2S-R6E-S29	
"	Greenhouse—Ann Arbor	T2S-R6E-S21	
"	Beach of North Lake	T1S-R4E-S18	
Wayne	Detroit		Hatch '39

digenous to the region, were made on that part of the island.

Armadillidium nasatum Budde-Lund

This species, which is here reported from the state for the first time, has been collected in only one locality—greenhouses of the University of Michigan Botanical Gardens, Ann Arbor, Washtenaw County. This isopod has been reported as far north as London, Ontario (Ross 1914) and as far west as Mt. Pleasant, Iowa (Longnecker 1924). In greenhouses in Michigan it was found with *Armadillidium vulgare*, which was as abundant outdoors as in these buildings. *A. nasatum*, however, was never found outside of the greenhouses, although inside it was as common as *A. vulgare*.

AQUATIC SPECIES

Asellus communis Say

Records which are available at the present time

AQUATIC SPECIES



FIG. 18. Distribution within the counties of Michigan of *Asellus communis* Say, *Asellus intermedius* Forbes, *Mancasellus danieli* (Richardson) and *Mancasellus tenax* (Smith). (For key to abbreviations of county names see explanation of Fig. 15.)

appear to indicate that this is the most abundant freshwater isopod in Michigan. It appears to be distributed throughout most of the state (Fig. 18). Van Name (1936) reports it to be "by far the most abundant and widely distributed fresh-water isopod in the eastern half of the United States." In Michigan, it has been collected in many different aquatic environments (Table 7). It has been found in trout streams, creeks, roadside ditches, drainage ditches, and rivers, in springs, swamps, millponds, permanent woodland ponds, temporary ponds and lakes. In Michigan, it usually was found on the bottom among detritus, or clinging to aquatic vegetation, or in mats of filamentous algae. However, *A. communis* also occurred under rocks in rapid streams. Only once was this species found swimming, but in this case—a woodland pool—it was very abundant and constituted the principal animal life of the pool.

TABLE 7. Michigan Records of *Asellus communis* Say.

COUNTY	LOCALITY	LOCUS KEY	REFERENCE
Cass	Michigan Crystal Springs		Richardson '05
Cheboygan	Carp Creek at Burt Lake	T36N-R3W-S4	UMMZ
"	Douglas Lake	T37N-R3W-S33	Dendy '44
Emmet	Maple River at Power Dam	T36N-R4W-S10	
Gratiot	Alma		UMMZ
Kent	Grand Rapids		Smith 1874
Manistee	Bar Lake	T24N-R16W-S15	
Marquette (UP)	Mill Pond, Marquette		UMMZ
"	Frismore Pond, Marquette		UMMZ
Oakland	Woodland Pond, Bloomfield		UMMZ
Schoolcraft (UP)	Pelkner Lake, Blaney Park		UMMZ
Washtenaw	Woodland Pond, Ann Arbor		UMMZ
"	Stream, White's Woods		UMMZ
"	Geddes Pond, Huron River	T2S-R6E-S26	
"	Pool, U. of M. Campus	T2S-R6E-S29	
"	Delhi Rapids, Huron River	T2S-R5E-S2	
"	Roadside Pool, Ypsilanti	T3S-R7E-S5	
"	Swamp, Liberty & Zeeb Rds.	T2S-R5E-S27	
Wayne	Creek, Redford Golf Course		UMMZ

Asellus intermedius Forbes

Although its distribution in North America is not as well known as that of *Asellus communis*, since reported records are rather few, *A. intermedius* is known to occur from the vicinity of Brunswick and Portland, Maine (Norton 1909) as far west as Omaha, Nebraska (Pearse 1913). In Michigan, it has been collected from Washtenaw County in the south to Cheboygan County and Bois Blanc Island in the north (Fig. 18). In my collections, there are specimens from lakes, springs and swamps (Table 8). It has been collected in situations similar to those habitats described for *A. communis*. Usually there is but one species of aquatic isopod for any

TABLE 8. Michigan Records of *Asellus intermedius* Forbes.

COUNTY	LOCALITY	LOCUS KEY	REFERENCE
Cheboygan	Spring, Straits Mackinac	T39N-R3W-PC334	
"	Roadside Park Spring	T38N-R2W-S6	
Grand Traverse	Boardman Lake		UMMZ
Grafton	Alma		Pearse '13
Mackinac (UP)	Duncan Lake, Bois Blanc Is.	----	
Muskegon	Muskegon Lake		UMMZ
Washtenaw	Steere's Swamp—Ann Arbor		Pearse '12
"	Swamp, Liberty & Zeeb Rds.	T28-R5E-S27	

particular habitat. However, in a swamp in Washtenaw County both *A. communis* and *A. intermedius* were collected in approximately equal numbers. Johansen (1920) and Van Name (1936) have pointed out the possibility that there two species may not be distinct.

Mancasellus danielsi Richardson

This isopod has been reported previously only from Indiana and Illinois. The Michigan records, based on specimens in the University of Michigan Museum of Zoology, are from the upper peninsula—Tahquamenon River, Luce County and Gulliver Lake, Schoolcraft County (Fig. 18).

Mancasellus dilatus (Smith)

There is only one record—the original—of this species for Michigan. It was collected on the Detroit River at Ecorse in Wayne County (Smith 1874).

Mancasellus tenax (Smith)

According to available data, *M. tenax*, which is second only to *Asellus communis* in abundance in Michigan, appears to be limited to the Great Lakes region. The localities in this state from which it has been collected are scattered over the lower peninsula (Fig. 18). Creeks, rivers, large and small lakes were found to be inhabited by this species (Table 9). It frequents the bottoms of shallow waters, occurring under logs and debris. Like other freshwater isopods, this species has been seen crawling on stems and under surfaces of leaves of submerged aquatic vegetation.

A few of the previous Michigan records for *Mancasellus tenax* are somewhat confusing. Among the localities for this species cited by Richardson (1905) are "Lake Superior; . . . Michigan; Lake Huron." However, she does not state where in these extensive areas the specimens were collected. Pearse (1910), in his "Preliminary List of the Crustacea of Michigan," quotes these three records of Richardson in his table of Michigan localities for this species. Although Richardson does not say where she obtained her data, the lake records were probably based on those of Smith (1874) which is the only paper prior to 1905 that lists these localities. The Lake Huron specimens were taken from

TABLE 9. Michigan Records of *Mancasellus tenax* (Smith).

COUNTY	LOCALITY	LOCUS KEY	REFERENCE
Michigan	Lake Huron		Richardson '05
Alpena	Thunder Bay, Lake Huron		Richardson '05
Benzie	Big Platte Lake		Smith 1874
Cheboygan	Black Lake		UMMZ
"	Creek S. of Cheboygan	T37N-R1W-S8	UMMZ
"	Maple River at Burt Lake		
"	Mouth of Nigger Creek	T36N-R3W-S32	
Chippewa (UP)	Whitefish Point	T36N-R2W-S16,17	
Menominee (UP)	Baker Lake		Hankinson '16
"	Bass Lake		UMMZ
"	Becker Lake		UMMZ
"	Lake Ann		UMMZ
Presque Isle	Black Lake		UMMZ
"	Clear Lake	T37N-R2E-S1	
Van Buren	North Lake		UMMZ

Thunder Bay (Smith 1874), and therefore their record is a legitimate one for Michigan. However, Smith made his Lake Superior collections off the shores of the island of Saint Ignace and in waters around the Slate Islands, all of which are located in the Canadian part of the lake. It would appear, therefore, that the Lake Superior record of Pearse is a doubtful one for Michigan. For these reasons, this particular record has not been included in the present Michigan records of this species.

HABITAT SELECTION

Although our knowledge of the distribution in Michigan of terrestrial isopods is not complete, there are sufficient data available to warrant a discussion of the preferences of certain species for specific habitats and of their general distribution throughout the lower peninsula. Some isopods have been found in many different types of situations throughout the area. Others are more particular and appear to be limited to several distinct environments or occur only in certain regions of the state, while a few ordinarily are found only in one particular type of habitat.

The lower peninsula of Michigan may be divided into three regions in respect to the terrestrial isopod fauna of the state. The southern section extends as far north as Bay City on the east, and Muskegon on the west. The northern district borders Lake Michigan, the Straits of Mackinac and Lake Huron, but it does not extend inland for any great distance except along the water courses. It consists of parts of Leelanau, Grand Traverse, Antrim, Charlevoix, Emmet, Cheboygan and Presque Isle Counties. The third area comprises the remaining central counties. There are few records of terrestrial isopods from this middle district. The reason for this is to be found in the nature of the region. Much of this part of the state is sparsely settled and has been burned over several times. The area is now characterized by jack pine uplands. The great majority of invertebrate animals usually associated with ter-

restrial isopods are absent from the region. *Tracheoniscus rathkei* was the only species found in most of the district, and it was not as abundant there as elsewhere. In this area occasional individuals of *Porcellio scaber* and of *Cylisticus convexus* were obtained along river banks and in towns, but these specimens were rare. Isopod populations in the northern and southern regions were larger than those in the central section.

Some of the terrestrial isopods appear to be restricted to the southern part of the state; others are more abundant in the south, but are occasionally to be found in the north; and still others are widespread in their distribution throughout most of the state (Fig. 19). *Porcellionides pruinosus* has been collected only in the southeastern section of Michigan, and *Ligidium longicaudatum* is known from only three southern counties. On the other hand, *Armadillidium vulgare* occurs as far north as Bay City and once was found as far north as Douglas Lake. This particular instance has been discussed previously. Between Bay City and Douglas Lake it is not known. Among the species that are distributed throughout the state are the three common isopods *Cylisticus convexus*, *Porcellio scaber* and *Tracheoniscus rathkei*. The factors that limit the distribution of terrestrial isopods may be climate or the influence of man.



FIG. 19. Distribution in Michigan according to counties of the fifteen species of isopods known to occur in the state. (For key to abbreviations of county names see explanation of Fig. 15.)

The majority of terrestrial isopods are said to be natives of Europe that have been introduced on this continent. This probably accounts for their abundance around human settlements—farms, public beaches, parks, cities and towns. In these places most of the terrestrial forms are to be found. In Michigan, the typical habitat for the three species *Armadillidium vulgare*, *Oniscus asellus* and *Porcellionides pruinosus* is around dwellings. Occasion-

ally *Cylisticus convexus*, *Porcellio scaber* and *Tracheoniscus rathkei* also occur here, but generally are not as numerous. All seven of these species have been collected in dwellings as well as out-of-doors.

Along various types of lake shores as well as along different types of river and stream banks one finds different species of isopods. *Cylisticus convexus* has been found on protected rocky beaches and river banks. It usually inhabits the middle beach. In Michigan, according to available records, this particular situation is preferred by this species. Here it occurs frequently and usually in large numbers. *Tracheoniscus rathkei* and *Porcellio scaber* are also found on rocky shores of lakes and rivers, but are scattered and are never as numerous as *Cylisticus convexus*. On the other hand, on sandy, debris-littered shores, *Porcellio scaber* is the predominant species. It, however, prefers the outer beach in such situations. If the lake or stream is in a well populated district *Armadillidium vulgare* may be found along it, but on sparsely settled shores it was not collected.

In areas that are usually wet, but not subject to flooding, such as certain marshlands, *Ligidium longicaudatum* will be found. In Michigan, although seldom collected, all specimens of this species were taken from such regions. *Trichoniscus demivirgo* also prefers a wetter situation than do most of the other terrestrial isopods. It has been found around Ann Arbor in deciduous woodlands under leaves and stones, in ditches or well protected places that are usually wet.

Stoller (1902) is of the opinion that the common name "Woodlouse," if applied to any isopod, should be used for *Tracheoniscus rathkei*. In Michigan, it, more than any other species, is a woodland form. As previously stated, it is to be found in the great majority of deciduous woods of the lower peninsula, where it is the predominant isopod. However, an occasional *Porcellio scaber* or *Cylisticus convexus* may be found along the margins of deciduous woods. If the wooded area is wet *Trichoniscus demivirgo* may occur.

There are at least two types of Michigan woodlands that typically do not harbor isopods. These are the aspen woods and the coniferous forests. The animals usually associated with terrestrial isopods are also absent from many of these areas. Aspen woodlands are generally dry, and this may explain in part the absence of isopods.

LIFE HISTORY STUDIES OF FOUR TERRESTRIAL SPECIES

HISTORICAL

Calman in 1911 wrote, "Although woodlice are very common animals, comparatively little is known of their habits." This statement is still applicable today, and especially is it true for our American forms. As previously stated, it is thought that many of our terrestrial isopods originated in the Old World, and therefore, the results obtained from biological investigations carried out in Europe for

these particular species may possibly be pertinent for our fauna. However, it has been only within recent years that the many specialists working on this group in Europe have emphasized their biology. One of the pioneer European papers on life history studies of these isopods was that by W. E. Collinge (1915). The paucity of previous publications of this nature is strikingly shown in Collinge's bibliography of five rather short articles. K. W. Verhoeff, an outstanding systematist of the group, has contributed much to the present status of our knowledge of them. A. Vandel, working on the genetics of terrestrial isopods, reported various phases of natural history that he encountered in his studies in France. H. W. Howard (1940), also primarily interested in isopod genetics, described, in general, the life history of *Armadillidium vulgare*. Several European publications on distribution, genetics and taxonomy of the group contain scattered bits of information on natural history, but these data are meager and far from complete.

Inasmuch as there have been only a few students of Isopoda in America, we are far behind Europe in our knowledge concerning them. The American specialists, for the most part, have been primarily interested in taxonomy or experimental biology and have almost completely neglected other biological aspects, especially the life histories of these crustaceans. Among the first American papers to deal with their general biology was Richardson's "Contributions to the Natural History of the Isopoda" (1904). This paper largely emphasized marine forms and gave only generalities for the terrestrial group. Probably one of the more important American articles was Pierce's "Notes on the Economic Importance of Sowbugs" (1907). Life history data of three isopods (*Armadillidium vulgare*, *Porcellio laevis*, and *Porcellionides pruinosus*) are given in his discussion on their depredations to crops around Dallas, Texas. Although much has been written concerning the reactions of certain species to light, moisture, contact and similar phenomena (Abbott 1918, Allee 1923, 1926, Brooks 1942, Miller 1938, and others) very little is known concerning the rest of their biology. The present investigation, therefore, extends our knowledge of the life histories of four common terrestrial species.

MATERIALS AND METHODS

The terrestrial isopods selected for study in the laboratory were chosen because they were abundant around Ann Arbor and were able to thrive under laboratory conditions. They were *Armadillidium vulgare* (Latreille), *Cylisticus convexus* (De Geer), *Porcellio scaber* Latreille, and *Tracheoniscus rathkei* (Brandt). For the most part, the present studies were based on animals raised in the laboratory, but field observations were made to substantiate laboratory results.

Several workers have described methods for raising sowbugs, but all had certain limitations as far as the present problem was concerned. Collinge

(1915) used glass observational cells similar to those employed in raising ants. Abbott (1918) reared his specimens in covered glass dishes containing earth, dry leaves and bark. Fuller (1937) recommended glass-covered, wooden boxes big enough to accommodate a thousand animals. Howard (1940) used "one pound jars with metal screw caps" as well as Petri dishes 10 cm. in diameter containing wet filter paper. During the present investigation, Abbott's method with certain modifications was used for rearing general cultures. Pulverized soil to a depth of one inch was placed in large, round, glass dishes. Raw potato, potato peelings, carrot or lettuce, as well as dried leaves and twigs were used for food. To provide adequate moisture and shelter for the animals, a folded paper towel saturated with water was added. Such containers, when covered with glass, were very satisfactory because they required attention only about once a month or even less frequently. The moisture was easily controlled by wetting the paper towel.

However, during this study, it was necessary to isolate many individuals and to keep them in containers which could be left unattended for a week or longer, and easily transported. Petri dishes containing wet paper, as suggested by Howard and others, were tried, but in our laboratory they did not prove satisfactory. It was difficult to control the humidity in these dishes and they were too small for some of the studies that involved rearing an entire brood in one container.

A plaster cup was finally devised which has proved very satisfactory. The container is 9.5 cm. in outside diameter and 6 cm. in outside height; its bowl is 4 cm. deep and 5.5 cm. in diameter. A groove is cut into the inner margin of the lip, thus allowing a glass cover to fit snugly. These containers were placed in pans of water, and by controlling the depth, the humidity inside the cups could be regulated. The water level in the pans is about the only thing that required attention, and inasmuch as the plaster cups are absorbent, it was not necessary that it remain constant. In fact, the water usually was not replaced until most of it had evaporated.

PERIODS OF GRAVIDITY

Isopods are considered to be gravid when they are carrying eggs, embryos, or young in their marsupia. The period of gravidity, therefore, extends from the time the eggs are first deposited in the marsupium until the young leave it. Inasmuch as the young may quit the brood pouch of their own volition, or the female may break it open and release all the young at once, there is considerable variation in length of time the young remain there. Apparently the young find the opening of the brood pouch only by trial and error; some remain behind as long as a week after the others have left.

Verhoeff (1919) found that for *Porcellio scaber* the period of embryonic development in the marsupium was 35 days, and that the period of larval development there lasted 16 days; that is, the com-

plete gravidity period was 51 days. However, during the present investigation it was found that females of this species were gravid for as short a term as 36 days, while one carried her brood for 57 days. For the 23 females whose periods of gravidity were definitely determined, the average was 43.5 days (Table 10). Usually, it took the second and third broods as long to develop as it did the first. This was not always the case, however, since in one instance the first gravidity period lasted 52 days, and the second only 36 days. All of these females were raised in the laboratory under as uniform conditions as possible.

TABLE 10. Broods of Isopoda Raised in the Laboratory.

Species	Size Range (Lengths in mm.)	Number Young in Brood		Days of Gravidity	
		Range	Average	Range	Average
<i>Armadillidium vulgare</i>	9.5 - 10.5	5 - 53	21	37 - 45	
	11.0 - 12.0	19 - 49	29	37 - 46	
	12.5 - 13.5	5 - 62	37	44 - 51	
	Totals.....	9.5 - 13.5	5 - 62	37 - 51	43
<i>Cylisticus convexus</i>	11.0 - 12.0	10 - 30	16	44 - 56	
	12.5 - 13.5	21 - 40	26	48 - 59	
	14.0 - 15.0	16 - 40	28	54 - 62	
	17	30	30	?	
	Totals.....	11.0 - 17.0	10 - 40	44 - 62	52
<i>Porcellio scaber</i>	9.5 - 10.5	6 - 37	19	36 - 52	
	11.0 - 12.0	6 - 40	23	36 - 57	
	12.5 - 13.5	17 - 42	40	41 - 46	
	15	40	40	48	
	Totals.....	9.5 - 15.0	6 - 42	36 - 57	43.5
<i>Tracheoniscus rathkei</i>	8.0 - 9.0	8 - 15	12	35 - 42	
	9.5 - 10.5	7 - 22	16	36 - 42	
	11.0 - 12.0	7 - 29	17	36 - 42	
	12.5 - 13.5	6 - 25	19	?	
	Totals.....	8.0 - 13.5	6 - 29	35 - 42	39

Pierce (1907) found that *Armadillidium vulgare* around Dallas, Texas, had an incubation period varying from 56 to 93 days, and Howard (1940) states that for this species it was between two and three months in England. In Michigan, females of *A. vulgare* raised in the laboratory were observed to carry broods from 37 to 51 days and the average period of gravidity was 43 days (Table 10).

Females of *Cylisticus convexus*, in general, carried broods longer than any of the other species, since they were gravid from 44 to 62 days, averaging 52 days (Table 10). On the other hand, females of *Tracheoniscus rathkei* were gravid for shorter periods than the other species. They carried broods from 35 to 42 days, with an average gravidity period of 39 days (Table 10).

In southern Michigan, gravid females of terrestrial isopods are found out of doors from the middle of March until the early part of August. As would be expected, the period of gravidity for this group living in the northern part of the lower peninsula begins later, around the latter part of May, and

usually extends through August. Inasmuch as many females have only one brood per year, the number of gravid females in the first part of the season is greater than at any other time. In the case of *Cylisticus convexus*, which usually has two broods per season, there are two periods in which gravid females are numerous.

Terrestrial isopods collected in the fall and reared in the laboratory have a much earlier period of gravidity than those left under natural conditions. The females usually begin carrying eggs around the first part of December and give birth to young from the latter part of that month through March. If a second mating occurs, females may be gravid as late as the first week of June.

BROODS

Number per Season

Not only is there a difference between the number of broods per season according to species, but for some, the number varies according to locality. For example Vandell (1939) working at Toulouse, France, found that *Armadillidium vulgare* produced three broods a year, whereas Howard (1940) states that the same species had but one brood in England. Eleven of the 18 females of *A. vulgare* raised in the laboratory during the present investigation had only one brood each. On the other hand, four had two broods, two and three broods and one even had four broods.

Twenty-eight females of *Cylisticus convexus* were studied to ascertain the number of broods during a season. Some of these were collected around Ann Arbor in the southern part of the state, others along the shores of Douglas Lake in the northern part of the lower peninsula. Animals taken from the two localities acted approximately alike. Fewer than half of them (12) had two or more broods. One of this group had three broods from one mating, and several others carried eggs in their marsupia for a third time, but these failed to develop. Some of the females from which only one brood left the marsupium carried eggs for a second time during the same season, but these never completed development. In Germany, according to Verhoeff (1919), this species generally has two broods. Females of a population of *Cylisticus convexus* studied in nature at the University of Michigan Biological Station had two periods of gravidity, but there were fewer gravid females during the second period than during the first.

Of the 19 females of *Porcellio scaber* whose broods were studied, ten had only one brood in a season, six had two, and three had three broods. It is usual for this species in central Europe to have three broods per season (Verhoeff 1919). Four of the nine females having at least two broods could not have mated between broods, because they were isolated even from their own young as soon as these left the marsupia. The other five might have mated with their progeny of the first brood, provided these young, from which they were not isolated, could

have become sexually mature within the six months which separated the two broods. Most young reach adult size at five months of age, and may be considered sexually mature. Consequently males of the first brood could have mated with their mothers. It should be pointed out, however, that Howard (1940) has shown that spermatozoa may live in the seminal receptacles of the females for as long as one year, hence, we cannot be sure in these cases of females not isolated from their progeny, whether the second brood was produced by an earlier mating or by mating with one of their offspring. This is one of several problems that will require further research.

Most females of *Tracheoniscus rathkei*, that were isolated when they first became gravid, had only one brood. Only six of them had two broods, and one had three groups of young. In this last case, however, the female could have mated with young of the second brood, from which she was not isolated. In contrast to these findings, Verhoeff (1919) found that in Europe this species usually had two broods per season.

From available data, it appears that in Michigan these isopods when raised in the laboratory have at least one brood per season, and occasionally more. However, *Cylisticus convexus* usually has two broods per season, although some of the second broods never develop beyond the egg-stage. An occasional female of any of the four species may have three broods per season. One female of *Armadiidium vulgare* produced four groups of young from one mating, and therefore had more broods than any of the others.

Number in Brood Pouch

It was feasible to study the number of eggs and other developmental stages in the marsupia of only one of the species under consideration, because the other three did not occur in sufficient numbers at any one time to warrant treating them statistically. Large aggregations of *Cylisticus convexus* were found along the shores of Douglas Lake during the summers of 1941 and 1942. From these, 141 gravid females were studied. Forty were collected July 5, 1941 and the remainder on July 7, 1942. Inasmuch as the number of eggs carried by the females collected in 1941 easily fell within the range of those carried by the 1942 animals, they have been grouped together. Only those isopods whose brood pouches had not been opened and therefore still contained the original number of eggs, embryos or young were considered. Only a few of the many females examined met this requirement, so that a relatively small number of individuals (141) was studied (Table 11). It was not possible to ascertain whether these females were carrying their first or second broods of the season.

The specimens were measured alive, but their broods were examined later after the animals had been killed and preserved. The length of the body was regarded as the distance from the anterior part of the head to the posterior margin of the telson. Width was taken at the widest place—the mid-

thoracic region. Roughly, width times length was considered to be the area of the body through the median plane. Measurements were made only to the nearest half millimeter, because the state of contraction of the body segments varied at least that much with individuals.

The eggs, embryos, and young in each marsupium were counted separately. Undeveloped eggs were found rather frequently, although the rest of the eggs in the brood had developed normally. In one instance, over half of the eggs had failed to mature, while the others had reached late embryonic stages when killed. In no instance, however, were eggs, embryos and young all present in one marsupium. The failure of some eggs to develop accounts for the fact that the number of eggs always exceeds or at least equals the number of young produced. The smallest brood consisted of 10 and the largest brood of 70. The second largest brood was composed of 63 individuals, while the third largest was 58. The average number per brood was 33.

The lengths of adult females varied from 10 to 17 mm., and widths ranged from 3 to 7½ mm. The area of body through the median plane for the smallest female was 30 sq. mm., and the corresponding area of the largest one was 119 sq. mm. There were some individuals both in the 1941 and the 1942 groups carrying eggs just beginning to cleave. Others had young ready to leave the brood pouch. However, the majority of isopods studied were carrying developing embryos. This apparently was due to the time of year when the collections were made. Broods of some females, as previously shown, may develop faster than broods of other individuals. More than likely all animals analyzed did not mate at the same time. Therefore, the rate of development of eggs as well as the time of mating of the parents determined the state of the individuals in the marsupia when the females were killed.

The smallest brood (10) was produced by the smallest female (10 x 3 mm.), and the largest brood (70) was from the second largest female (17 x 6.5 mm.). In general, there was a positive relationship between area of body through the median plane and size of brood (Table 11). This is clearly evident in Figures 20 and 21: the former is a correlation table which plots area of body through the median plane of the 141 females in relation to size of their broods, and the latter is the curve derived by grouping these data and plotting the mean. There are slight fluctuations, but this last curve approaches a straight line. The correlation coefficient, +0.75, between body area and number per brood, indicates that the size of a brood is largely dependent on the size of the female.

In order to contrast the size of an individual brood of a terrestrial isopod with that of an aquatic species, females of *Asellus communis* were obtained from Bar Lake, Manistee County on April 17, 1941. Inasmuch as only 50 females had unopened brood pouches, this study had to be based on a smaller group than was the previous part. Most members of

TABLE 11. *Cylisticus convexus* (De Geer). Number of Eggs, Embryos or Young in Marsupia in Relation to Size of Female.

No. of Indiv. in Group	Size Ranges in mm.			Ranges of Numbers in Marsupia					
	Area of Median Plane	Length	Width	Eggs	Em- bryos	Young	Total		
9.....	30 - 39.5	10 - 11	3 - 4	1	13 - 23	10 - 27	10 - 28	19	
33.....	40 - 49.5	10 - 12	4 - 4.5	1 - 11	12 - 28	13 - 37	13 - 39	22	
20.....	50 - 59.5	12.5 - 14	4 - 4.5	1 - 18	15 - 33	11 - 46	14 - 48	27	
12.....	60 - 69.5	11 - 13.5	4.5 - 5.5	1 - 3	15 - 36	46 - 48	15 - 48	29	
39.....	70 - 79.5	14 - 15	5 - 5.5	1 - 42	18 - 46	19 - 47	18 - 50	36	
8.....	80 - 89.5	14.5 - 16	5 - 6	1 - 44	37 - 50	51	40 - 52	45	
15.....	90 - 99.5	14 - 16	6 - 6.5	1 - 52	32 - 54	..	32 - 63	47	
3.....	100 - 109.5	16 - 17	6 - 6.5	1	44 - 54	..	44 - 55	50	
2.....	110 - 119.5	17	6.5 - 7	3	54 - 70	..	57 - 70	63	

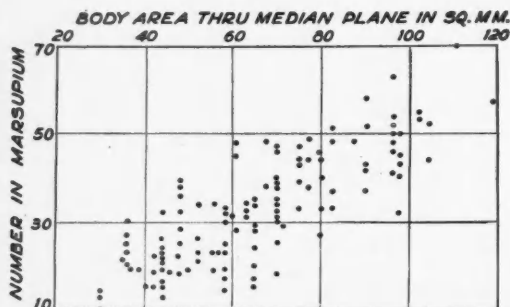
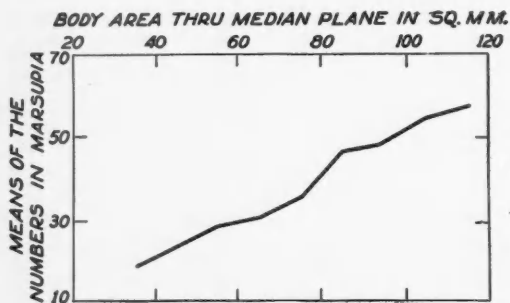
FIG. 20. Correlation table of body area through median plane and number of individuals in marsupium of 141 females of *Cylisticus convexus* collected during the summers of 1941 and 1942 from the shores of Douglas Lake, Michigan.

FIG. 21. Curve obtained by grouping data from Fig. 20 and plotting the means.

a brood were in approximately the same developmental stage, but uncleaved eggs were also found. Table 12 groups the lengths of females and the numbers in their broods. Length was measured to the nearest half millimeter, but was taken after the animals had been killed and preserved. Females varied in size from 7 to 11 mm. in length. Broods of *Asellus communis* collected in Michigan were much larger than those of *Cylisticus convexus*. The average brood of the 50 aquatic females was 117. Number per brood ranged from 53 to 235 (Table 12).

The 235, however, appears to be an exceptionally large number of young, because the second largest consisted of only 194.

As in the case of *Cylisticus convexus*, the smallest brood of *Asellus communis* was from the smallest female—53 young from an individual 7 mm. long. The largest brood (235) was from a female 10.5

TABLE 12. *Asellus communis* Say. Number of Eggs, Embryos or Young in Marsupia in Relation to Length of Female.

Grouped Lengths (in millimeters)	Number in Group	Ranges of Numbers in Marsupia			
		Eggs	Embryos	Young	Total
7 - 7.5.....	3	..	53 - 63	70	53 - 70
8 - 8.5.....	4	3 - 146	89 - 98	..	73 - 146
9 - 9.5.....	29	1 - 122	72 - 160	90 - 164	73 - 168
10 - 10.5.....	12	1 - 235	72 - 168	93 - 133	72 - 235
11 - 11.5.....	2	143 - 185	143 - 185

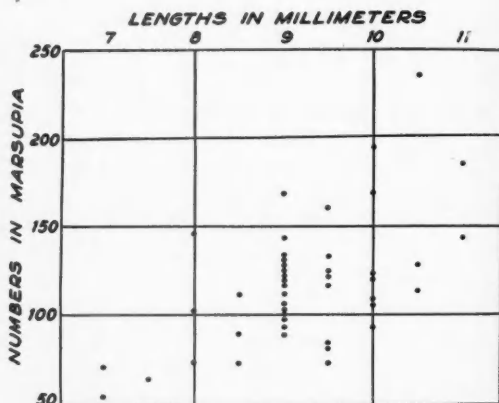
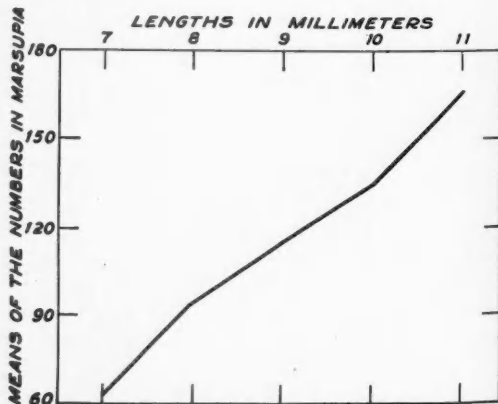
FIG. 22. Correlation table of length and numbers of individuals in marsupia of 50 females of *Asellus communis* collected April 17, 1941 from Bar Lake, Manistee County, Michigan.

FIG. 23. Curve obtained by grouping data from Fig. 22 and plotting the means.

mm. long. Only two of the 50 females were longer (11 mm.) than this. There is a positive correlation between the length of body and number of young in a brood for this species also (Table 12), the correlation coefficient being + 0.7. Figure 23 is the curve obtained by grouping the data from the correlation table (Fig. 22) and plotting the means of these groups. This curve is almost a straight line, except for slight fluctuations at either end. Therefore, these data indicate a rather close relationship between length of female and number of individuals in her marsupium.

Number of Young That Leave Marsupium

There was a great range in the number of young that left the brood pouch. Not only was there considerable difference in numbers according to species, but large variations existed among individuals of the same species. However, for all Isopoda studied the time of year had no influence on the number of young in a brood.

Pierce (1907) found that *Armadillidium vulgare* around Dallas, Texas, produced from 29 to 79 young per brood. Collinge (1915) reported that individuals of this species from Scotland, raised in captivity, had broods of 50 to 150. He once obtained 267 young from one brood. In France, this species had broods varying from 48 to 156 (Vandel 1939). During the present investigation, it was found that females of *A. vulgare* collected around Ann Arbor had anywhere from 5 to 62 young per brood (Table 10), and the average was 28. When females had two or more broods during one season, the broods usually were approximately equal. The largest number of young (139) borne by a single female during an entire season was from an individual which had four broods. One of the factors which influenced the number of young per brood was the size of the female. For *A. vulgare* a positive correlation with a coefficient of + 0.75 existed between the length of the mother and the number of young she produced in one brood.

The smallest number of young to leave the marsupium of a female of *Cylisticus convexus* was ten (Table 10). One female from Ann Arbor and another collected along the shores of Douglas Lake had broods of this minimum size. Of the 28 females of *C. convexus* which were studied the largest brood was 40, while the average was 24. The number of young produced by a single individual for an entire season ranged as high as 86. Females with broods containing fewer than 15 young usually had other broods during that season.

In a preceding section it was shown that the number of eggs, embryos and young, whatever combinations of these three stages occurred in a marsupium, may range as high as 70 for *C. convexus*. However, the largest number of young actually in a single pouch was 51 (Table 11). Eggs, embryos and young, combined, averaged 33 per brood, while on the average only 24 young left the pouch from a single brood. There is, therefore, a considerable difference

between the number of eggs first placed in the marsupium and the number of young to leave it. When the female releases her brood, the undeveloped eggs may be extruded from the marsupium by violent contractions of the body so that the oostegites are forced apart, or, if the female is undisturbed and the young leave the pouch of their own volition, then the undeveloped eggs may remain in the marsupium until the individual molts and they are cast off in the old exuviae.

There was a positive correlation between the length of a female of *Cylisticus convexus* and the number of young in a single brood that leave her marsupium alive. The coefficient for this correlation was + 0.69. In a previous section, it was shown that there was a greater correlation (+ 0.75) than this between the body area through the median plane of females of this species and the number of eggs produced. Failure of all eggs to develop may account for some of the difference between these two coefficients. Another possibility to consider is that length of female alone may not be indicative of the number of young, but that area of body through the median plane based on width as well as length is a better criterion for predicting number of offspring from a single brood.

Collinge (1915) found that females of *Porcellio scaber* raised in the laboratory produced broods of only 12 to 30 young, but in Germany Verhoeff (1919, 1920) recorded broods that averaged 88 individuals. Females of this species in Michigan had broods that ranged from 6 to 42 young (Table 10), and the average was 24. The largest number of young produced by a single female during one season and from only one mating was 89 from a total of three broods. Second and third broods of the season usually had the same number of young as did the first one. However, there were some exceptions to this. A positive correlation, with a coefficient of + 0.71, existed between area of body through the median plane and number of offspring produced in a single brood of *P. scaber*.

According to available data from 28 females, *Tracheoniscus rathkei* had smaller broods than the other three species studied. These isopods also had the shortest periods of gravidity. Broods of *T. rathkei* varied from 6 to 29 young (Table 10), and the average was 17. When one female had more than one brood, usually the number of offspring was about the same for each brood. Two females, both of which mated but once, produced 56 young each during one season. This was the largest number borne by any female of this species during a single season. Although a positive correlation was found to exist between size of female and number of young in a single brood, this correlation was not as significant for this as for the other three species, since the correlation coefficient was only + 0.58.

YOUNG

Females carry not only eggs and developing embryos in their marsupia, but during the last weeks

of gravidity their brood pouches also contain young. The pouch is constructed of five pairs of overlapping plates which extend inward from the bases of the first five pairs of legs (Van Name, 1936). This overlapping of the oostegites allows the marsupium to expand as the developing brood requires more room. When the young are ready to leave the female, the oostegites may barely touch each other, or small gaps may even show between the plates along the mid-ventral line. At this time, the exit from the marsupium first appears as an opening at the anterior edge of the pouch, usually located on the ventral surface of the first thoracic segment. Young of the four species studied become rather active and move around just preceding their departure. In their activity, the young find the anterior opening of the marsupium, or one of the gaps between the oostegites through which they may leave. During the departure of the young the female usually remains relatively quiet. If she is active at all, she moves very slowly, keeping the first pair of legs immobile. The young customarily emerge from the brood pouch head first and climb around on the ventral surface of the female. Most of them descend from their mother by way of her first two pairs of legs. The majority of the young after leaving their parent are not very active and remain together in a group. Towards the end of the emergence period, the female moves away from the young. This time all legs are used, and the motion of the moving female usually forces the few remaining young out of the marsupium. The above is customary when the female is not disturbed. However, if she is agitated while carrying young in her pouch she may, by rhythmical contractions of her body, force apart the pairs of plates forming the marsupium and release all her brood at once. A brood pouch full of young makes it necessary for the female to move around rather slowly and in a humped position; after the release of the brood she assumes her normal position and moves about more quickly.

Pierce (1907) stated that the young of *Armadillidium vulgare* undergo their first molt within 24 hours after leaving the marsupium. During the present investigation this was the case for the great majority of young of this species, as well as those of *Cylisticus convexus*, *Porcellio scaber*, and *Tracheoniscus rathkei*. However, some molted within 12 hours after they left the female, and others were 64 hours old before they molted the first time. It is only after the first molt that the young become very active. Up to this time they are usually sluggish and tend to remain near the place where they were deposited.

When the young leave the marsupium, they are whitish in color and are somewhat translucent. Soon after their first molt they change to a pale yellow, and from this time on gradually become darker with age. Although young were never found feeding before their first molt, they begin eating shortly after this ecdysis. At this stage in their development they are so translucent that their gut, full of food, is clearly apparent as a dark mid-dorsal line.

Many habits described for the adults are possessed by the young soon after they leave the marsupium. Immature isopods are very gregarious, forming large aggregations. Young of the same size and age usually tend to group together, avoiding the older animals. Young isopods probably are even more cannibalistic than are the older ones. It is not at all unusual to see larger members of a brood feeding upon smaller ones, especially while the latter are molting. Sometimes as many as half of the brood are used for food by the other young. Most of the smaller members of a brood remain runts even if isolated. They seldom attain a length of 5 mm. in a period as long as 30 weeks, so that if they escape their larger brothers in nature they probably never become sexually mature. The ability to roll up into a compact ball is possessed by all young of *Armadillidium vulgare* and *Cylisticus convexus*, even during the day they leave the pouch. Immatures of all four species can feign death as do the adults—ventral side up, legs partially out-stretched, body motionless.

MOLTING AND GROWTH

The procedure, customarily employed by terrestrial isopods, of molting first the posterior part of the exuviae, followed by shedding the anterior portion, is rather unique and has, therefore, attracted considerable interest (Casserley quoted by Webb, 1900; Pierce, 1907; Aubin, 1914; Mosley, 1915; Verhoeff, 1940). The line separating these body divisions usually is located between the fourth and fifth thoracic segments, but in certain individuals the break may occur between the third and fourth thoraxes. However, it was found to be constant for a particular individual.

During the present investigation over 50 broods of four species (*Armadillidium vulgare*, *Cylisticus convexus*, *Porcellio scaber*, and *Tracheoniscus rathkei*) were studied to determine the approximate time-interval between the first several molts. These individuals were isolated and were provided with abundant food. As previously stated, the young usually molted for the first time within 24 hours after leaving the marsupium. It was observed that the second molt usually took place within the first two weeks after birth, and that most individuals molted for the third time during the third week. The majority of young underwent the fourth molt during the fifth week, but some were molting as early as the fourth week and others as late as the sixth. Beginning with the fourth instar most of the young underwent a molt every two weeks until they were approximately 20 weeks old. After this period molts were very irregular. The above is not in accordance with Pierce (1907) who found that there was no regularity of molts after the first one; instead, the time of molt was dependent upon the food supply.

Females usually undergo a molt within a few days prior to placing eggs in the marsupium. Probably the oostegites are released by this molt, and form the brood pouch. Shortly after the young leave the pouch the female molts again, forming another

pouch if she is to have another brood. These two molts occur even if the female has not mated, in which case the sterile eggs pass into the marsupium and remain there for as long as a month. However, they begin degenerating within the first week after deposition. When they are shed during the next molt, these eggs are very shriveled and are lumped together into two compact groups, each of which formerly extended the whole length of the marsupium.

Aubin (1914) found that the majority of individuals of *Porcellio laevis* did not hide before molting, but rather remained with the group. This observation, however, is at variance with the data on the four species studied by the present writer. When an adult of any of these species is ready to molt it seeks a protected location on a rough surface. It then becomes rather sluggish and does not feed. A definite break in the exoskeleton occurs in the mid-thoracic region and the posterior portion of the exuviae appears very loose. Every few seconds the animal contracts its body, thereby gradually pulling out of the exuviae. In the final phases of this half of the molting procedure, the isopod by more violent contractions finally comes out of the posterior portion of the exuviae, usually leaving it in one piece adhering to the substratum. This process may take only 15 minutes, but some animals have been observed to take as long as six hours for it. After molting, the posterior part of the animal is dull, while the anterior half, still covered by the old exoskeleton, is glossy. Usually, at first, the part just molted is narrower than the rest of the body.

A few minutes after the first phase of molting, the isopod begins to move about slowly, using the legs that have not molted. A usual procedure at this time is for the animal to eat its exuviae. However, Aubin (1914) states that individuals of *Porcellio laevis* do not feed upon their cast-off exoskeletons. The isopod remains in seclusion until after the anterior half of the old integument is shed.

Within three days after the posterior molt, the anterior one occurs. Shortly after the animal has devoured the first part of the molted exuviae, the old exoskeleton of the anterior part becomes loose from the body. This time, the animal by slow contractions of the body backs out of the exuviae, which again may be left in one piece. For a while the animal moves only on the legs freed during the first half of the molt, but soon it is using all of them. It usually eats most of the anterior portion of the exuviae before it returns to a group. Approximately a week is required for the entire molting process of an adult, beginning when the individual leaves the group and ending with its return. This period, however, is much shorter for the growing, immature individuals. Many isopods were found dead with the anterior exuviae only partially removed. Others molted, only to die within the next few days.

As previously stated, the first three molts take place a week apart, but beginning with the fourth

ecdysis and continuing at least through the eleventh molt, the animals shed their integuments on the average at bi-weekly intervals. A sudden increase of body length may take place after an ecdysis, or the molt may result in only slight increase in size, or even in no growth. During the early weeks of development, regardless of molting, a gradual lengthening of the body occurs. However, in later life an increase in length usually follows a molt, and between molts the animal remains about the same size.

The majority of individuals of all four species studied exhibit certain general tendencies in their development. Many young are approximately 2 mm. long at birth. For most of them a period of rapid and steady growth begins with the first molt. This gradual increase in body size continues until the animal is approximately 8.5 mm. long. Some individuals, however, may not stop their steady growth until they are 10 mm. in length (Fig. 27), and on the other hand animals of minimum size may cease their uniform development when much smaller. Following the period of rapid increase in size, the isopod grows at a slower and somewhat irregular rate. Still later in life, growth generally occurs only with an ecdysis. However, molting does not always result in measurable increase in size.

The curves (Figs. 24-27) showing the rate of growth of the four terrestrial species are based on individuals that lived fifteen weeks or longer. These animals were individually isolated until death, and were measured weekly, beginning with emergence from the marsupium. Some grew very rapidly (Maximum curve, Fig. 26), while others remained stunted. Isopods of this last group, seldom attaining a length of 5 mm., were not considered in drawing the above curves, because in nature they probably do not survive. In order to demonstrate the increase in length during a particular week among individuals of the same species, excluding runts, the extremes in size were plotted as well as the mean length.

Some periods of molting can be noticed in the "staircase effect" in the curves showing increase in lengths of animals of maximum and minimum size. However, times of molting in the early developmental period for *Porcellio scaber* and *Tracheoniscus rathkei* are not as noticeable as are the early ecdyses of *Armadillidium vulgare* and *Cylisticus convexus*. Individuals of *Porcellio scaber* (Fig. 26) had the most uniform rate of development of all the species studied, and *Cylisticus convexus* had the slowest rate of development. Many individuals of *Tracheoniscus rathkei* (Fig. 27), on the other hand, attained most of their growth much earlier than did the individuals of the other species.

The longest life-span reported for any terrestrial isopod is that recorded by Geiser (1934) for *Porcellio laevis*, the males of which, he states, may live as long as five years. Pierce (1907) writes that an individual *Armadillidium vulgare* which he collected "was probably several years old." Howard (1940) records this last species as living at least two years,

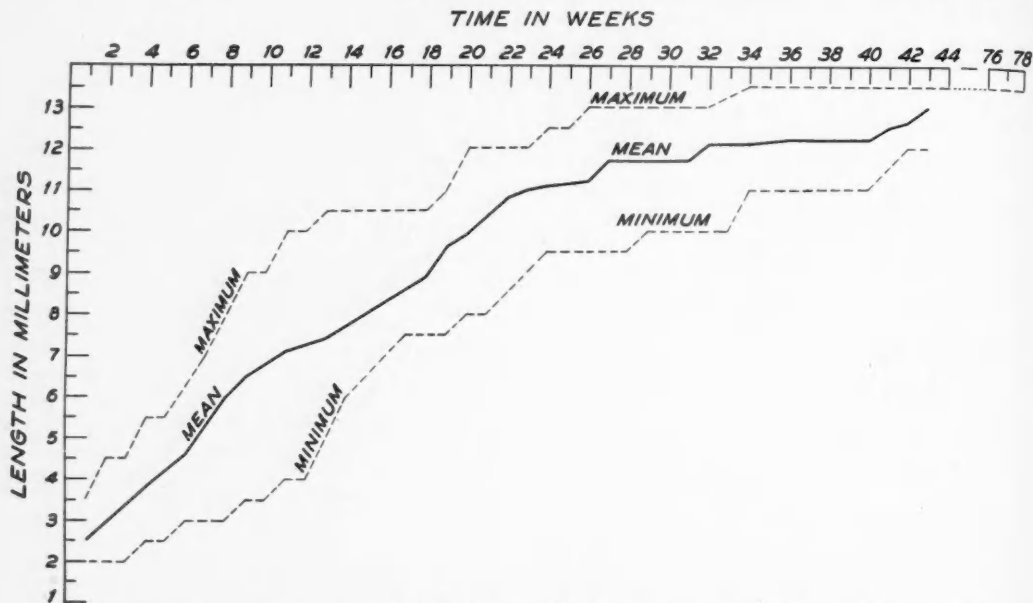


FIG. 24. Increase in length among individuals of *Armadillidium vulgare* (Latreille), showing growth of animals of maximum and minimum size as well as mean growth for all individuals studied.

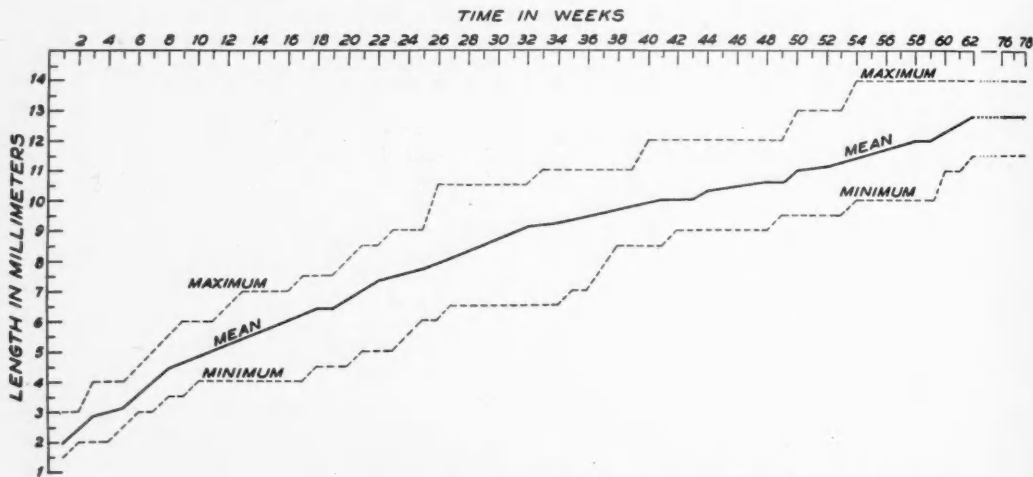


FIG. 25. Increase in length among individuals of *Cylisticus convexus* (De Geer), showing growth of animals of maximum and minimum size as well as mean growth for all individuals studied.

and states that during this period both males and females are sexually potent. Although maximum ages of the four terrestrial species considered in this investigation were not determined, certain data on their longevity were obtained. The present observations ran over a period of three years, but none of the individuals studied survived that long. It appears that isopods raised in the laboratory from females collected in Michigan have a life-span of approximately two years. Howard's (1940) observations in England on *Armadillidium vulgare* are

in agreement with this. It was also found that isolated males of all four species lived in the laboratory as long as the females. This is not in accord with the findings of Geiser (1934) who states that members of one sex, depending on the species, may live longer than those of the opposite sex.

AN ISOPOD POPULATION

PREVIOUS STUDIES

The literature dealing with populations of the Oniscoidea is rather limited. There have been two

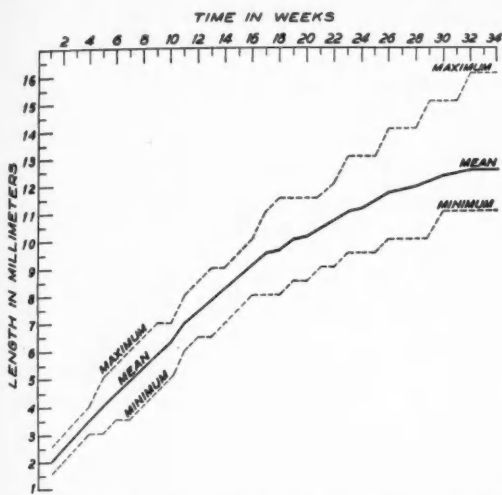


FIG. 26. Increase in length among individuals of *Porcellio scaber* Latreille, showing growth of animals of maximum and minimum size as well as mean growth for all individuals studied.

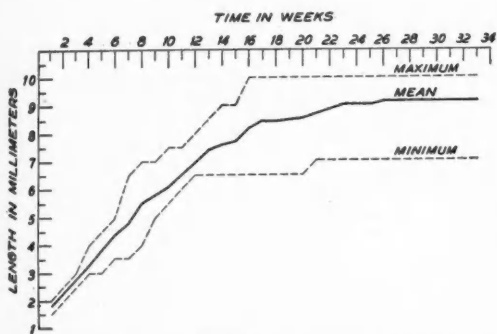


FIG. 27. Increase in length among individuals of *Tracheoniscus rathkei* (Brandt), showing growth of animals of maximum and minimum size as well as mean growth for all individuals studied.

groups of workers interested in isopod populations. One group has studied aggregations of certain species, and from experimental data has obtained explanations of bunching among these animals. The other workers have analyzed populations of various species in order to determine sex-ratios and to interpret differential longevity in relation to sex. Studies of aggregations and distribution according to sex have been, in general, the chief contributions to the analysis of populations of this group of animals.

MATERIALS AND METHODS

The paucity of papers dealing with populations of isopods led the author into this field of endeavor. Sex-ratios of the species selected had not been determined. Nothing was known concerning variations of size in relation to various external factors, nor had periods of gravidity been studied within a large

population. These three aspects, therefore, were chosen for emphasis.

On the west shore of South Fish-Tail Bay, Douglas Lake, there stretches a narrow rocky beach along the outer edge of which rise steep wooded slopes. During the summer months, *Cylisticus convexus* occurs in great abundance under stones and driftwood on this beach. These animals do not ascend the slope, but are confined, principally, to the middle beach with an occasional individual to be found in the outer beach. The population of *Cylisticus convexus* occurring in this region was selected for study because individuals of all sizes were abundant in this limited area.

Inasmuch as it was not feasible to study this entire population, various sampling methods were used. Potato traps made according to Geiser (1928) were tried, but proved unsatisfactory because some of them were carried off by mammals and others were filled with spider webs and seldom contained isopods. A square sampler made of sheet metal, each side of which was one half meter long, was devised so that it could be pushed down into the sand; the stones removed from the enclosed area; and the trapped animals picked up. This sampler worked very well along that part of the shore where pebbles and stones were not abundant, but where they were plentiful it was difficult to use. A final method, although somewhat cruder than the use of the sampler, proved more satisfactory. An area of one fourth square meter was marked off on the beach. The stones within this area were carefully removed, beginning at the periphery and working toward the center. In order to escape, the isopods had to cross the cleared spaces and could be picked up easily. Such areas were laid off at five-meter intervals along the length of this particular part of the shore. As soon as the isopods had been removed from a sample area, the rocks and debris were replaced.

Collections were made at weekly intervals during the four summers of 1939 through 1942. No attempt was made to have weekly collections contain the same number of individuals, but rather, each collection was taken from 20 sample areas located in the middle beach. The very young which were unpigmented were not taken since they were indistinguishable from those which were forced from brood pouches when gravid females were crowded into collected bottles. Isopods were gathered before 10 A.M. and were measured during that same day. Subsequently they were killed and preserved in a mixture of nine parts 70% ethyl alcohol and one part glycerine containing a few milliliters of glacial acetic acid.

Length of an individual was measured from the anterior margin of the head to the posterior edge of the telson. The uropods were not included because many of the specimens lacked or were regenerating them. The animals were measured only to the nearest whole millimeter, because contraction and relaxation between segments of the body made more accurate measurement impracticable.

SIZE-FREQUENCIES

Weekly Variations

Histograms were plotted showing the size variations for each weekly collection during the four summers. Since all 33 of these figures showed certain similarities, only those for the summer of 1942 are presented as being typical of this pattern (Figs. 28-37). The great majority of them are bi-modal and for many of these the low point between the two modes occurs at 8.5 millimeters. There is, however, a definite tendency towards the end of each season for these curves to become uni-modal.

During each of the four summers from 1939 through 1942, the population of *Cylisticus convexus* exhibited certain similar phenomena in weekly changes of individual lengths. In the following paragraphs, therefore, the animals collected in 1942 are discussed as showing these typical changes. Weekly variations in size of individuals during that year are discussed later.

In early summer, the population is composed of two groups (Fig. 28). One group is made up of those large individuals that survived the winter; the other consists chiefly of their young born that spring. The older and longer isopods are in the majority during the early summer (Figs. 28, 29), but with the advent of the second brood of the year (Fig. 30) and the dying off of some of the older individuals, the younger group gradually becomes predominant (Figs. 30-33). The young of the first brood grow approximately one half millimeter per week, and it is not surprising, therefore, that longer animals again constitute the larger group (Figs. 34, 35). Toward the end of the season, members of the second brood have increased so much in length that it is no longer possible to distinguish them from others in the population (Figs. 36, 37).

This gradual change in size of animals of the first and second broods, and death of older individuals which survived the winter are clearly illustrated in the histograms. Early in the summer, the curves are broad and distinctly bi-modal (Figs. 28-34). The second mode, representing the older and longer individuals, is, for the most part, larger than the first mode based at first on the young of the first brood plus probably some of the runts that survived the winter, and later upon animals of both the first and second broods of the year. As the weeks pass, the first part of the bi-modal curve becomes predominant (Fig. 33), but in the following weeks, the second mode becomes larger again (Figs. 35, 36). Finally, when the members of the second brood of the season have attained a certain size, the population becomes rather homogeneous and is represented by a narrow uni-modal curve (Fig. 37).

The exact reason why a great many of these bi-modal curves have a low point at 8.5 mm. is not positively known. There is, however, a probable explanation. Only rarely do females of *Cylisticus convexus* in this locality become gravid before they are 8.5 mm. long. In 1941, less than one tenth of

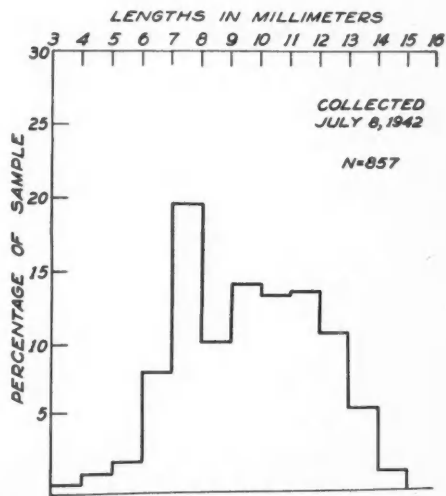
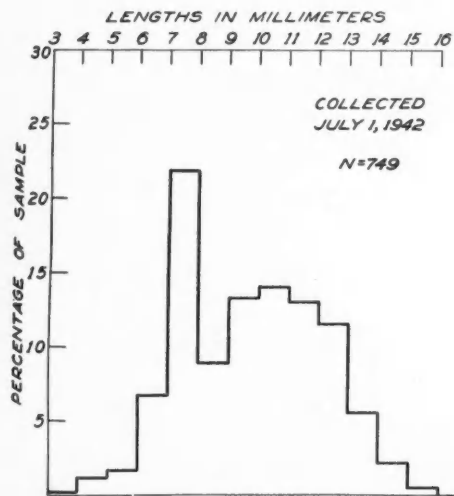
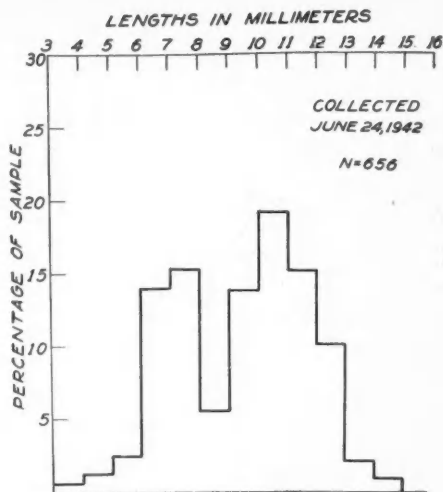
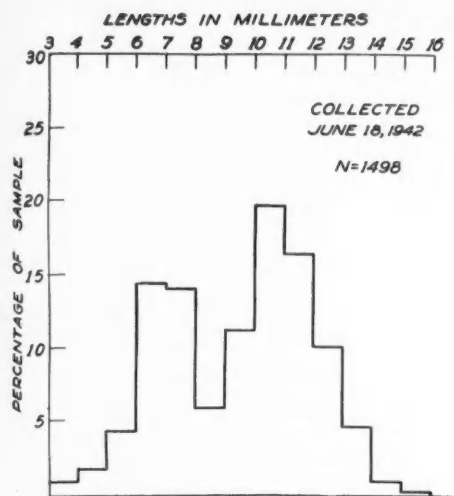
one percent of the gravid females were shorter than 8 mm., and during the summer of 1942 the corresponding group comprised only four tenths of one percent. Sexual maturity, then, for the females at least, is not attained until they are over 8 mm. in length. Most individuals raised in the laboratory, regardless of sex, molt after they have become 8 mm. long, and for many an appreciable increase in length follows this molt. Growth up until this time has been rather rapid and steady, but after this length is attained there is a much slower and rather erratic development. The first mode, therefore, of these bi-modal curves represents the immature individuals of the population; the second mode is based on mature specimens. The uni-modal curves which we get at the end of the summer (Fig. 37) show that at this time of the year most of the population has become mature. Runts that never will attain appreciable size are the exception and tend to broaden the curves at their beginnings.

During the summers of 1939 through 1941, weekly variations in lengths of individuals within the population underwent changes similar to those shown for 1942. However, there were certain minor differences. The population of 1939, as illustrated in the weekly samples, definitely consisted of two distinct groups only through July 18. After this date, the two divisions of the population were very difficult to separate. Samples taken in the summer of 1939 did not consist of as many individuals as those of the following years. The irregularity in various size groups may be the result of these smaller samples. The chief difference between the population in 1940 and in 1942 is that the 1940 group became homogeneous after July 24, while the animals in 1942 could be divided into two distinct groups as late as August 12. The variations within the population during 1941 are very similar to those in 1942 which were considered in the previous paragraphs.

A few individuals in this population attained the length of 17 mm. These, however, were rare. On the other hand, most weekly collections contained isopods that were as long as 16 mm. The mean length of the population varied from week to week. During the summer of 1939 the maximum mean length was 10.2 mm., while the minimum mean length was 9.6 mm. In 1940 the mean length of the population ranged as high as 10.5 and as low as 9.8 mm. Mean length in 1941 varied from 10.4 to 8.0 mm., and in 1942 it was between 9.7 and 8.8 mm. This variation, however, is discussed more fully in the following section.

Seasonal Variations

Mean length of the population, based on weekly samples, varied from week to week during the summers of 1939 through 1942 (Fig. 38). These fluctuations, however, followed the same pattern for each of the four summers (Figs. 38, 39); the latter curve is based on measurements of approximately 24,000 animals. The mean length of the population increased in the early summer, and reached its maxi-

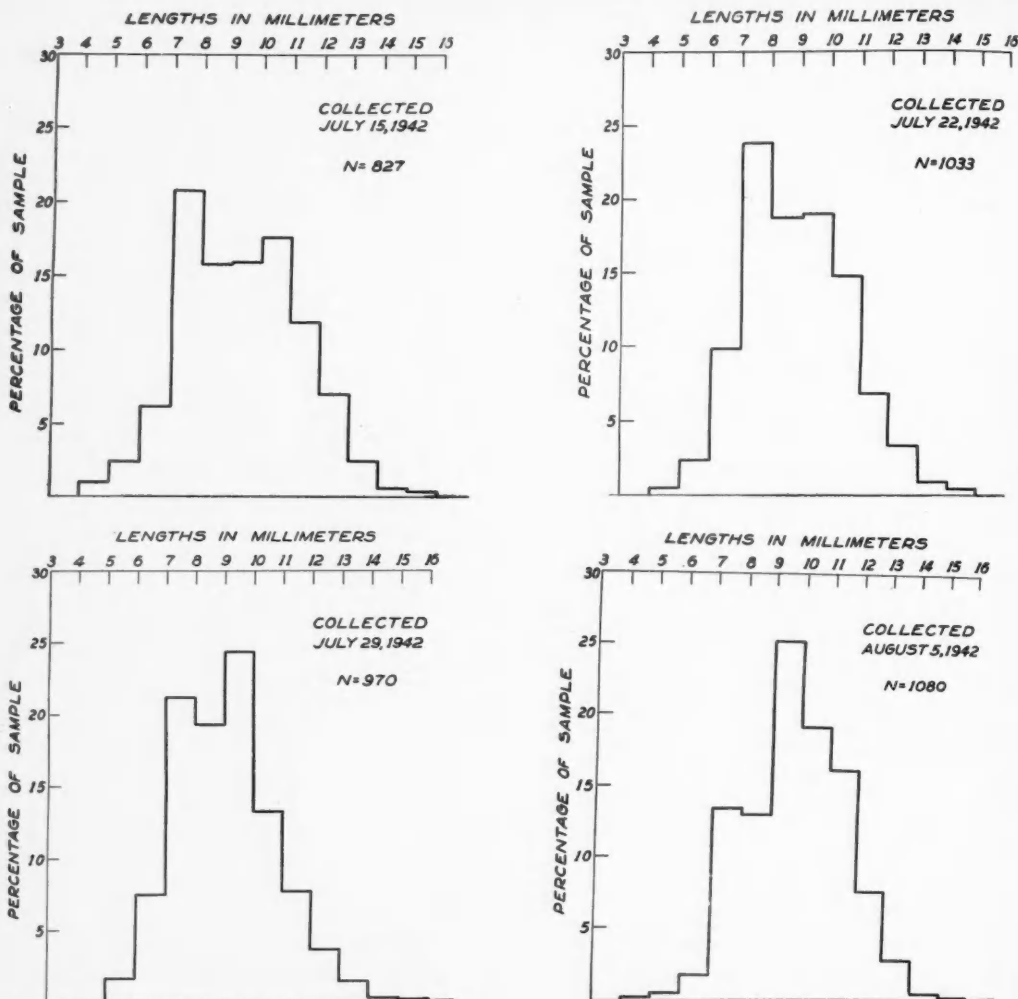


FIGS. 28-31. Size-frequency curves of body length of *Cylisticus convexus* collected during the summer of 1942 along the west shore of South Fish-Tail Bay, Douglas lake, Michigan.

mm between the last week of June and the second week of July. There followed a period of several weeks in which the mean length of the population decreased. This continued until the third or fourth week of July. After this, however, the mean length again increased, but at the end of the summer it began falling once more. Although there is not a great deal of variation in the mean lengths for any one summer, it is significant that similar variations recurred in the other three summers. The differences between the highest and lowest mean length, based on weekly collections, were 0.6, 0.7, 2.4, and 0.9 mm. for the respective summers of 1939 through 1942. Standard errors for the 33 weekly population samples ranged from 0.02 to 0.1 mm.

A possible explanation of this consistent variation

during each of the four summers is based on the interaction of at least four factors: the birth and the growth of young on the one hand, the stationary size and the death of older isopods on the other. Previous to the last week of June, 1941, a great many young were born and by the time they were collected in that week, they had grown to a measurable size and therefore greatly influenced the mean length of the population. In other years, this first brood did not appear as early as in 1941, so that its effect upon the size of the population as a whole was not felt until later in the season. During the molt following the release of a brood from the marsupium, many females die. Therefore, the death of the older and longer individuals, as well as the arrival of new broods, tends to lower the mean length



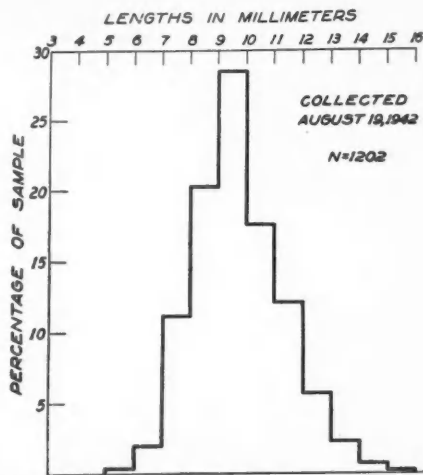
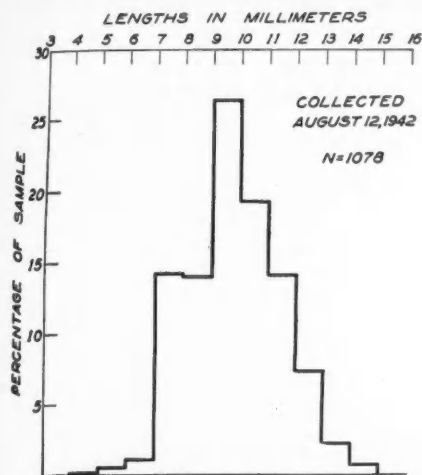
FIGS. 32-35. Size-frequency curves of body length of *Cylisticus convexus* collected during the summer of 1942 along the west shore of South Fish-Tail Bay, Douglas Lake, Michigan (continued).

of the entire population during the first three weeks of July. The young continue to grow, and with their continual growth the mean length of the population increases. During the last weeks of July, however, a second brood appears. Isopods from these second broods are found in the collections of the first week in August, and with their appearance the mean length of the population again decreases.

During early summer when mean length of the population is increasing, the animals fall into two distinct groups, the older and longer of which is predominant (Figs. 28-30). Following this period, however, the mean length decreases, and during these weeks the young and smaller animals are predominant (Figs. 31-33). With an increase of mean length in the succeeding weeks, the longer animals again become outstanding (Figs. 34, 35). The two groups,

however, cannot be distinguished easily from one another after the first week in August, when the mean length of the population again decreases (Figs. 36, 37).

Precipitation plays an important part in determining mean length of the population. Data for amount of rain that fell during the summer months when the University of Michigan Biological Station was in session were obtained from Dr. F. C. Gates. The rain gauge was located on the grounds of the Station, near the area within which the isopods were collected. Any effects of local inequalities of precipitation, therefore, were much less than they might have been if the gauge had been located far from the area from which the animals were taken. In summers when little rain fell, the size of most of the individuals was not as great as during rainy summers.



FIGS. 36, 37. Size-frequency curves of body length of *Cylisticus convexus* collected during the summer of 1942 along the west shore of South Fish-Tail Bay, Douglas Lake, Michigan (continued).

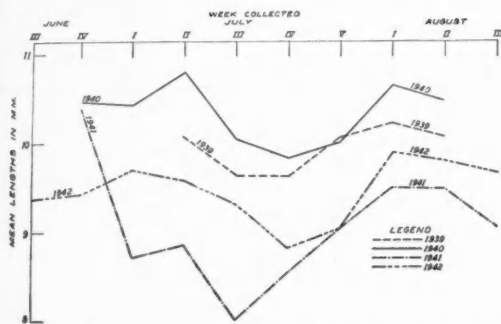


FIG. 38. *Cylisticus convexus*, variations in mean length of body during the summers of 1939-1942.

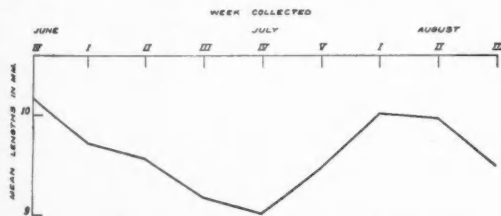


FIG. 39. Typical variations in mean length of body of *Cylisticus convexus* during the summer, based on animals collected at weekly intervals in 1939-1942.

During the summer of 1940 there was 6.18 inches of rain. More rain fell that summer than during any of the other three. It can be noticed from Fig. 38 that for 1940 the mean lengths were greater than for any of the other years. In 1939, 5.81 inches of rain fell, and isopods of that year were only slightly smaller than those of 1940. During 1941 the summer was dry, with only 1.96 inches of rain; correspondingly, individuals of *Cylisticus convexus* were smaller on the average than in the two pre-

ceding summers. The summer of 1942 was moderately dry, with 2.34 inches of rain, and isopods taken that summer were somewhat larger than those taken in 1941 but not as long as those collected in the summers of 1939 and 1940 when the precipitation was greater.

Temperature is another factor which undoubtedly influences growth of terrestrial isopods. Unfortunately, it was not possible to isolate it from other interacting factors without conducting experiments over a considerable period, and that did not seem feasible at that time. Temperature curves for each of the four summers were plotted against mean length curves, but it was not evident from these data how changes of temperature affect growth of isopods. In general, however, it can be said that, other things being equal, the effect of increased temperature within a narrow range results in an increase in body length two weeks later. Further study of this particular problem is needed before anything more than the above general statement can be made. Such a study should take into consideration humidity as well as temperature for both the microhabitat and the general environment. The author plans to undertake such an investigation at the earliest opportunity.

SEX RATIOS

The sex of individuals in each size-group of the 19 weekly sample-collections made during the summers of 1941 and 1942 was determined by studying the shape of the pleopods and by the presence or absence of external genitalia. Table 13 gives, for each week of the 1941 and 1942 seasons, the number and percentage of males and females within the various size-groups whose class limits are one millimeter. Distribution of both sexes according to size for each of these two summers, as well as totals for these groups, can be ascertained at a glance.

TABLE 13. *Cylisticus convexus* (De Geer). Size in Relation to Sex.

Summer of	Length in mm.	Number Males	Number Females	Total Number	Percentage Males	Percentage Females
1941....	3-4	3	3	6	50.0	50.0
	4-5	24	27	51	47.1	52.9
	5-6	98	100	198	49.5	50.5
	6-7	303	425	728	41.6	58.4
	7-8	543	735	1,278	42.5	57.5
	8-9	333	510	843	39.5	60.5
	9-10	485	704	1,189	40.8	59.2
	10-11	327	645	972	33.6	66.4
	11-12	172	637	809	21.3	78.7
	12-13	50	329	379	13.2	86.8
	13-14	13	142	155	8.4	91.6
	14-15	1	39	40	2.5	97.5
	15-16	0	9	9	0.0	100.0
	16-17	1	0	1	100.0	0.0
	Totals....	2,353	4,305	6,658	35.3	64.7
1942....	3-4	6	13	19	31.6	68.4
	4-5	23	37	60	38.3	61.7
	5-6	82	103	185	44.3	55.7
	6-7	333	379	712	46.8	53.2
	7-8	775	916	1,691	45.8	54.2
	8-9	551	744	1,295	42.5	57.5
	9-10	802	1,137	1,939	41.4	58.6
	10-11	438	1,233	1,671	26.2	73.8
	11-12	203	1,081	1,284	15.8	84.2
	12-13	63	682	745	8.5	91.5
	13-14	13	247	260	5.0	95.0
	14-15	1	72	73	1.4	98.6
	15-16	0	9	9	0.0	100.0
	Totals....	3,290	6,653	9,943	33.1	66.9

Females of several species of isopods appear to be more numerous than the males. Howard (1940) found in a collection of 380 *Armadillidium vulgare* taken around Cambridge, England, that 273 of them were females and only 107 were males. In other words, over 71% of this group was composed of females. Vandel (1925) also found a preponderance of females for several other species. Geiser (1934), working in Iowa and Texas, found that sexes are approximately equal in collections of *Tracheoniscus rathkei*, but that females are slightly more numerous in *Armadillidium vulgare* and *Porcellio laevis*. According to Geiser, the females of *T. rathkei* have a greater survival value than the males, while the males of *A. vulgare* and *P. laevis* live longer than the females.

During an eight-week period in the summer of 1940 a total of 3,807 individuals of *Cylisticus convexus* was collected along the west shore of South Fish-Tail Bay, Douglas Lake. Approximately 72% of these were females (Table 14). Of the 6,658 specimens gathered during nine weeks of the summer of 1941 nearly 65% were females. From collections made at weekly intervals over ten weeks of the summer of 1942 practically 67% of the 9,943 animals were females. Considering all 20,408 specimens taken during these three summers, slightly more than 67% of them were females (Table 14). In this particular population, therefore, the females were consistently predominant.

TABLE 14. *Cylisticus convexus* (De Geer). Weekly Variations of Sex.

Date Collected		Number Males	Number Females	Total Number	Percentage Males	Percentage Females
Year	Day					
1940	June 25	111	364	475	23.4	76.6
	July 3	85	364	449	18.9	81.1
	July 12	108	405	513	21.1	78.9
	July 17	157	319	476	33.0	67.0
	July 24	111	209	320	34.7	65.3
	July 31	169	328	497	34.0	66.0
	August 7	139	295	434	32.0	68.0
	August 14	190	455	645	29.5	70.5
1940 Totals....		1,068	2,739	3,807	28.1	71.9
1941	June 25	423	757	1,180	35.8	64.2
	July 2	208	268	476	43.7	56.3
	July 9	293	807	1,100	26.6	73.4
	July 16	270	450	720	35.8	64.2
	July 23	272	478	750	36.3	63.7
	July 30	178	392	570	31.2	68.8
	August 6	203	446	649	31.2	68.8
	August 13	213	374	587	36.3	63.7
	August 19	293	333	626	46.8	53.2
1941 Totals....		2,353	4,305	6,658	35.3	64.7
1942	June 18	367	1,128	1,495	24.5	75.5
	June 24	223	429	652	34.2	65.8
	July 1	282	467	749	37.7	62.3
	July 8	266	597	863	30.8	69.2
	July 15	237	586	823	28.8	71.2
	July 22	331	695	1,026	32.3	67.7
	July 29	377	596	973	38.7	61.3
	August 5	361	716	1,077	33.5	66.5
	August 12	377	708	1,085	34.7	65.3
	August 19	469	731	1,200	39.1	60.9
1942 Totals....		3,290	6,653	9,943	33.1	66.9
Three Summer Totals		6,711	13,697	20,408	32.9	67.1

The percentage of females varied from week to week during all three summers (Fig. 40; Table 14). Always, however, the females were predominant. Percentage of females in the summer of 1940 varied from 65.3 to 81.1; in 1941, from 53.2 to 73.4; and in 1942, from 70.9 to 75.5. These weekly variations for each of the three summers appear to show a definite trend. The females are most abundant early in the summer. Following this period, the percentage of females in the population continues to drop for several weeks. By the latter part of July, however, the females in the population apparently are increasing again, but at the end of the season they are not as plentiful as they were a few weeks previously. The variation in the percentage of females from week to week appears to be connected with periods of gravidity. A comparison of Figures 40 and 43 shows that shortly after the major period of gravidity early in the summer, when the females are most abundant, there is a decrease in the female population, and a similar decrease occurs again at the completion of the second period of gravidity. Many females of this species raised in the laboratory died during the molt that followed the departure of young from the brood pouch. It would appear that some of the females in this population from

the shores of Douglas Lake also died at the end of their gravidity period, and this would then account for the decrease of females in the sample collections which were made after the two periods of gravidity in nature. The increase in the percentage of females during the middle of the summer probably is the effect of the young from the first brood attaining measurable size. The introduction, therefore, of another group containing more females than males would tend to enlarge again the female population in comparison with that of the males.

species. In the population of *Cylisticus convexus* studied during the present investigation, the females were consistently larger than the males (Figs. 41, 42; Table 13). The mean length of females at all times during the summers of 1941 and 1942 were greater than the mean lengths of males in this population. This sexual dimorphism was particularly striking each summer until the third week of July, but thereafter there was less difference between the two sexes in this respect.

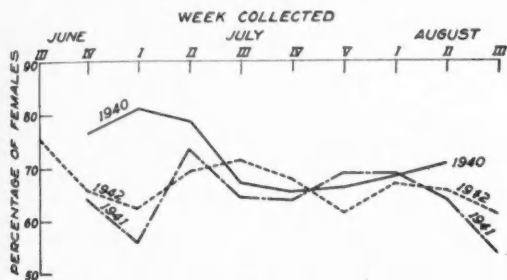


FIG. 40. Variations from week to week of the percentage of females in a population of *Cylisticus convexus* during three summers.

Vandel (1925) and Geiser (1934) state that for various species of terrestrial isopods the sexes are approximately equal in populations of the very young, even though later in life one of the sexes will become predominant. This might also be true for the population of *Cylisticus convexus* under consideration. However, females were generally slightly predominant even in the smallest size-group; the percentage increased with each succeeding group, so that the great majority of the larger individuals were females (Table 13).

According to Vandel (1925) males of many terrestrial isopods are generally smaller than females. He does not give any figures, however, to support this statement, nor does he specify any particular

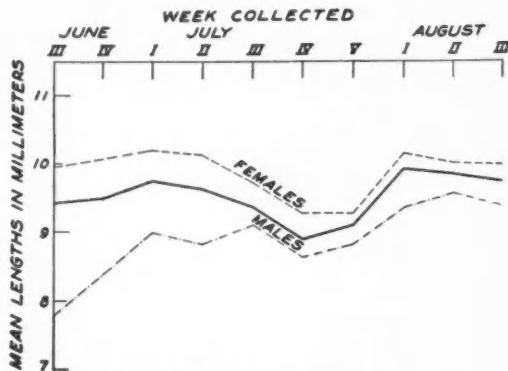


FIG. 42. Variation of mean length of males and females within a population of *Cylisticus convexus* during the summer of 1942.

GRAVIDITY

As mentioned in a previous section, animals were considered to be gravid when they were carrying eggs, embryos or young in their marsupia. Gravid and non-gravid females were separated in each size-group within the 19 collections made during the summers of 1941 and 1942. The numbers and percentages of each group for every weekly collection are listed in Table 15, in which all females collected during each summer are considered together according to the various size-groups. A very few females are mature when 7 mm. in length, but as pointed out previously most reach maturity when between 8 and 9 mm. long, so that it is in this size-group that the first gravid females appear in any significant number when considered as a group for an entire season (Table 15). There was a definite relationship between size of female and gravidity, since as the size of the individuals increased, the percentage in each size-group that were gravid also increased. For example, in 1941, all of the largest females were gravid, and 88.9% of the largest size-group in 1942 were also carrying eggs, embryos or young.

During the last week of June in the summer of 1940, 84% of the females were gravid (Table 16). Starting with the third week of July, however, the young began to leave their mothers, so that between 55 and 56% of the females were gravid on July 17. Finally during the fifth week of July, only slightly more than 14% of all females were carrying eggs or developmental stages in their marsupia. The

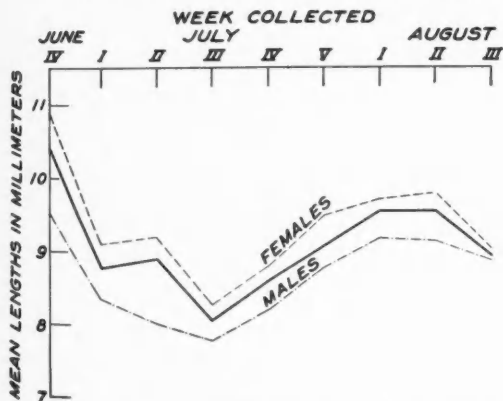


FIG. 41. Variations of mean length of males and females within a population of *Cylisticus convexus* during the summer of 1941.

TABLE 15. *Cylisticus convexus* (De Geer). Gravidity in Relation to Body Length.

Summer of	Length in mm.	Number Gravid	Number Non-Gravid	Total Number	Percentage Gravid	Percentage Non-Gravid
1941....	3-4	0	3	3	0.0	100.0
	4-5	0	27	27	0.0	100.0
	5-6	0	100	100	0.0	100.0
	6-7	0	425	425	0.0	100.0
	7-8	1	734	735	0.1	99.9
	8-9	39	471	510	7.6	92.4
	9-10	118	586	704	16.7	83.2
	10-11	181	464	645	28.1	71.9
	11-12	316	321	637	49.6	50.4
	12-13	243	86	329	73.9	26.1
	13-14	119	23	142	83.8	16.2
	14-15	38	1	39	97.4	2.6
	15-16	9	0	9	100.0	0.0
	Totals....	1,064	3,241	4,305	24.7	75.3
1942....	3-4	0	13	13	0.0	100.0
	4-5	0	37	37	0.0	100.0
	5-6	0	103	103	0.0	100.0
	6-7	0	379	379	0.0	100.0
	7-8	10	906	916	1.1	98.9
	8-9	94	650	744	12.6	87.4
	9-10	422	715	1,137	37.1	62.9
	10-11	588	645	1,233	47.7	52.3
	11-12	633	448	1,081	58.6	41.4
	12-13	445	237	682	65.2	34.8
	13-14	160	87	247	64.8	35.2
	14-15	54	18	72	75.0	25.0
	15-16	8	1	9	88.9	11.1
	Totals....	2,415	4,239	6,653	36.3	63.7

second brood of that year was found in the pouches during the first week of August.

In the last week of June, when the first collection was made during the summer of 1941, practically 78% of all females gathered were gravid (Table 16), but in the following week many broods left their mothers' pouches and only about 42% of the females were carrying broods. Young continued to leave their mothers during the next two weeks, so that on July 16 only approximately 3% of the females collected were gravid, and most of these were in the larger size-groups. After this date, however, the second broods began to appear in the marsupia, so that almost 5% of the females were gravid on July 23. The number of gravid females continued to rise as more and more of them began carrying their second brood for that year, so that on August 13 slightly more than 36% of the females were gravid. In the following week, however, the second brood of young began leaving the marsupia, and only about 14% of the females were gravid.

In the summer of 1942, more of the females (69.9%) were gravid on June 18 than at any other time during that year (Table 16). The number of gravid females remained about the same during the following week (69.0%), but after that many young began leaving the pouches, and on July 1 only 57% of the females were still carrying broods. During the next two weeks most of the young left their mothers, and on July 15 approximately 10% of all

TABLE 16. *Cylisticus convexus* (De Geer). Weekly Variations in Gravidity of Females.

Date Collected		Number Gravid	Number Non-Gravid	Total Number	Percentage Gravid	Percentage Non-Gravid
Year	Day					
1940	June 25	307	57	364	84.3	15.7
	July 3	310	54	364	85.2	14.8
	July 12	335	70	405	82.7	17.3
	July 17	177	142	319	55.5	44.5
	July 24	35	174	209	16.7	83.3
	July 31	47	281	295	14.3	85.7
	August 7	67	228	295	22.7	77.3
	August 14	45	410	455	9.9	90.1
1940 Totals....		1,323	1,416	2,739	48.3	51.7
1941	June 25	589	168	757	77.8	22.2
	July 2	113	155	268	42.3	57.7
	July 9	44	763	807	5.5	94.5
	July 16	13	437	450	2.8	97.2
	July 23	21	457	478	4.4	95.6
	July 30	54	338	392	13.8	86.2
	August 6	46	400	446	10.3	89.7
	August 13	136	238	374	36.4	63.6
	August 19	48	285	333	14.4	85.6
1941 Totals....		1,064	3,241	4,305	24.7	55.3
1942	June 18	789	339	1,128	69.9	30.1
	June 24	296	133	429	69.0	31.0
	July 1	269	198	467	57.6	42.4
	July 8	286	311	597	47.9	52.1
	July 15	61	525	586	10.4	89.6
	July 22	122	573	695	17.6	82.4
	July 29	140	456	596	23.4	76.6
	August 5	176	540	716	24.5	75.5
1942 Totals....	August 12	170	538	708	24.0	76.0
	August 19	105	626	731	14.4	85.6
Three Summer Totals		4,801	8,896	13,697	35.1	64.9

females were gravid. Beginning on July 22, however, more females (17.6%) were pregnant with their second broods of the season. In the following weeks the percentage of gravid females increased, but with the departure of young from these second broods, the number of females that were gravid began to decrease.

During these three summers the females of *Cylisticus convexus* became gravid early in June or late in May. Young of 2 mm. in length were found outside brood pouches as early as the second week of June. During the latter part of June and the first weeks of July the great majority of the mature females were gravid (Fig. 43). By the third week of July most of the young had left the brood pouches and only a few females still carried broods. Shortly after this, however, many of the females again became gravid. Not as many of the entire population, however, carried young this second time as earlier in the season. By the first or second week in August these females had deposited their broods, and following this period few females were gravid. Unfortunately the investigation was never continued beyond the third week in August, so that it is not known whether a third brood appeared.

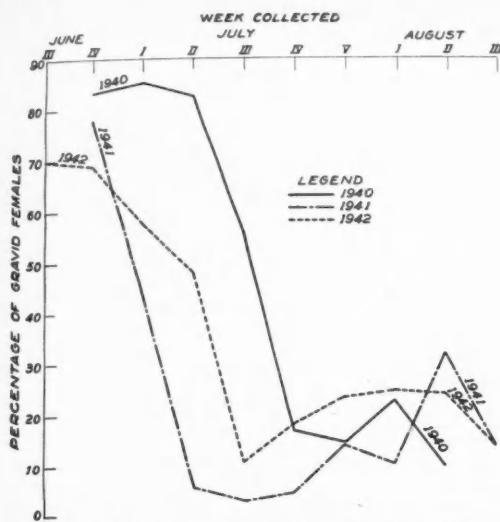


FIG. 43. *Cylisticus convexus*, Curves showing the two periods of gravidity during the three summers of 1940-1942.

Verhoeff (1919) states that in Germany females of *Cylisticus convexus* have their first broods during May and June, and that in July and August the second broods appear. This corresponds rather closely with what is known concerning this species at Douglas Lake, Michigan (Table 16). Many of the females of the population of *C. convexus* from the shores of this lake have two broods during a summer. Young of the first brood appear during the first weeks of July, and the second brood arrives in the latter part of August. These two periods of gravidity are clearly illustrated in Fig. 43, which shows the percentage of females that were gravid each week of the summers of 1940 through 1942. Early in the summer the majority of females are mature, since they were born the previous year and have lived through the winter. Most of them are gravid late in June and early in July (Table 16). By the time the second period of gravidity occurs, young of the first brood have appeared in the collections, and inasmuch as they have not had time to become mature they are not gravid. They tend to decrease, therefore, the percentage of females carrying young during the second period of gravidity. Accordingly, second modes on the curves in Fig. 43 are not as high as they would have been had it been possible to exclude immature females from the collections.

SUMMARY

(1) The objectives of the investigation were to determine which species of isopods occur in Michigan, their distribution within the state, as well as their habitat preferences; to work out as far as possible the salient features of the life histories of four terrestrial species; and to make quantitative

analyses of an isopod population in nature with respect to variations in size, sex, and other biological phenomena.

(2) Field work was begun during the summer of 1938 and continued through August 1942. Collecting trips were made into every county of the lower peninsula of the state.

(3) A total of 359 new locality records for isopods was established from 74 of the 83 counties of Michigan. Isopods were collected from all counties of the lower peninsula and in several localities of the upper peninsula.

(4) Fifteen species of isopods representing the suborders Oniscoidea and Asellota are now known to occur in Michigan. Four of these are here reported for the first time from the state. They are *Armadillidium nasatum* Budde-Lund, *Oniscus asellus* Linnaeus, *Trichoniscus demivirgo* Blake for the terrestrial species, and *Mancasellus danielsi* Richardson in the aquatic group.

(5) Check-lists and maps for the various species giving their distribution within Michigan are included. Distribution in the state for each species as it is now known is discussed.

(6) *Tracheoniscus rathkei* (Brandt), *Cylisticus convexus* (De Geer) and *Porcellio scaber* Latreille are generally distributed throughout the state and are the most abundant in the order named. *Oniscus asellus* Linnaeus and *Porcellio spinicornis* Say have been found in few and widely scattered areas in Michigan. *Armadillidium vulgare* (Latreille) occurs principally in the southern part of the state, and *Ligidium longicaudatum* Stoller and *Porcellionides pruinosus* (Brandt) are known in Michigan only from that section. *Armadillidium nasatum* Budde-Lund and *Trichoniscus demivirgo* Blake were collected only in Washtenaw County.

(7) From data now available, it appears that *Armadillidium nasatum* does not occur outside of buildings; *Armadillidium vulgare* is chiefly to be found around human habitations; *Cylisticus convexus* prefers rocky regions; *Ligidium longicaudatum* occurs in wet situations; *Porcellio scaber* lives on beaches, river banks and other moist situations; *Porcellio spinicornis* requires a habitat in which some form of lime is present; *Porcellionides pruinosus* is somewhat urban in its distribution; *Tracheoniscus rathkei*, although generally distributed, is more abundant in deciduous woodlands than elsewhere; and *Trichoniscus demivirgo* prefers moist woodland situations.

(8) A key to the fresh water and terrestrial isopods of Michigan is included.

(9) A method of raising terrestrial isopods in plaster cups is described.

(10) Gravidity periods for four terrestrial isopods were determined. The period for *Armadillidium vulgare* averaged 43 days. For *Cylisticus convexus* it varied from 44 to 62 days, and averaged 53 days. *Porcellio scaber* carried broods for an average of 44 days. Females of *Tracheoniscus rathkei* were gravid on the average for 39 days.

(11) Many females of *Armadillidium vulgare*, *Cylisticus convexus*, and *Porcellio scaber* have at least two broods a year, while *Tracheoniscus rathkei* females usually reproduce only once.

(12) The number of young, embryos and eggs from the marsupia of 141 gravid females of *Cylisticus convexus* were counted. The smallest brood consisted of 10 individuals, the largest of 70, and the average of 33.

(13) The number of individuals in a brood pouch of *Asellus communis* ranged from 53 to 235. The average brood contained 117.

(14) There is a positive correlation between body size of female and number of young she will produce.

(15) The number of young in broods of *Armadillidium vulgare* raised in the laboratory averaged 28; in broods of *Cylisticus convexus*, 24; of *Porcellio scaber*, 24; and of *Tracheoniscus rathkei*, 17.

(16) The departure of the young from their mother is described in detail. Habits of the very young are discussed.

(17) An isopod molts for the first time within 24 hours after leaving the marsupium. Second and third molts occur during the second and third weeks respectively. Beginning with the fourth instar, molts occur every two weeks until the animal is 20 weeks old. After this age the period between molts is irregular.

(18) Methods and habits of molting, as well as effects of molting on growth, are discussed.

(19) Growth of the four terrestrial species studied was steady and rapid at first, but after the isopod had become approximately 8.5 millimeters in length growth was much slower and somewhat irregular.

(20) It appears that many individuals of the terrestrial species studied may live to be approximately two years old.

(21) A population of *Cylisticus convexus* in nature was analyzed over a period of four summers. Approximately 24,000 individuals were studied.

(22) The population of *C. convexus*, from early summer to the middle of August, consists of two groups: an immature portion born that year, and mature individuals which are over 8.5 millimeters long. After the middle of August most of the population is mature.

(23) Variations in mean lengths of *Cylisticus convexus* for the summers of 1939 through 1942 followed a definite pattern, which may have been the result of death of older individuals and birth of new broods balanced against one another.

(24) The amount of rainfall appears to influence mean growth of the population. During summers when moisture was abundant mean length was greater than in seasons of drought.

(25) The sexes are about equally divided in that part of the population which is smaller than seven millimeters in length. In all other size-groups females are predominant. Sixty-seven percent of all specimens collected during the summers of 1940-1942 were females.

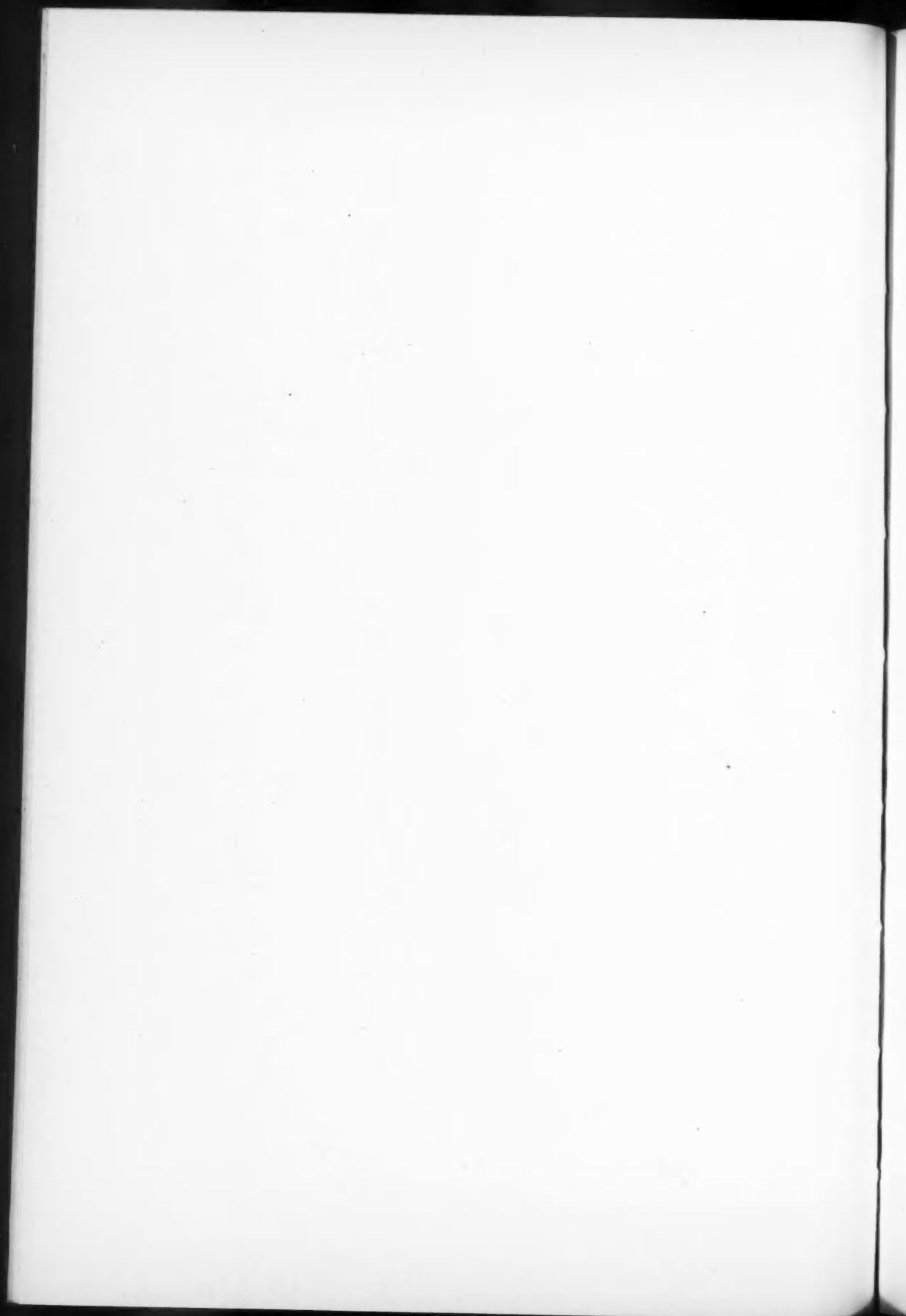
(26) Females of *Cylisticus convexus* in the population studied were longer than the males.

(27) *Cylisticus convexus* has two periods of gravidity. During the first period each summer the majority of females are gravid, but during the second period fewer than half of them carry eggs.

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A PHENOLOGICAL RECORD FOR SAUK AND DANE
COUNTIES, WISCONSIN, 1935-1945

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A PHENOLOGICAL RECORD FOR SAUK AND DANE COUNTIES, WISCONSIN, 1935-1945¹

INTRODUCTION

Each year, after the midwinter blizzards, there comes a thawing night when the tinkle of dripping water is heard in the land. It brings strange stirrings, not only to creatures abed for the night, but to some who have been asleep for the winter. The hibernating skunk, curled up in his deep den, uncurls himself and ventures forth to prowling the wet world for breakfast, dragging his belly in the melting snow. His track marks one of the earliest dateable events in that cycle of beginnings and endings which we call a year.

From the beginnings of history, people have searched for order and meaning in these events, but only a few have discovered that keeping records enhances the pleasure of the search, and also the chance of finding order and meaning. These few are called phenologists.

The events comprising the annual cycle are innumerable. Wisconsin, for example, has about 350 species of birds, 90 mammals, 174 fishes, 72 amphibians and reptiles, 20,000 insects, and 1,500 higher plants. The life of each of these 22,000 species consists of a sequence of events, each a response to the advancing season. No one phenologist can hope to recognize, much less to record, more than a very small fraction of this prodigious drama.

Many of the events of the annual cycle recur year after year in a regular order. A year-to-year record of this order is a record of the rates at which solar energy flows to and through living things. They are the arteries of the land. By tracing their responses to the sun, phenology may eventually shed some light on that ultimate enigma, the land's inner workings.

Yet it must be confessed that with all its weighty subject-matter, phenology is a very personal sort of science. Once he learns the sequence of events, the phenologist falls easily into the not-very-objective role of successful seer and prophet. He may even fall in love with the plants and animals which so regularly fulfil his predictions, and he may harbor the pleasant illusion that he is "calling shots" for the biota, rather than vice versa.

Phenologists are a heterogeneous lot, and have found shelter under diverse intellectual roof-trees. Thoreau (1906), the father of phenology in this country, scorned any roof-tree but his own; hence his records (for the period 1850 to 1861) remained unpublished for half a century. Hough (1864) was a doctor of medicine, and the Bureau of Patents published his tables. Henry (1881) was an agronomist and a dean; the Board of Regents published

his reports. Hopkins (1918) was an entomologist; the Weather Bureau published his findings. Among contemporary phenologists are botanists, foresters, game managers, ornithologists, range managers, and zoologists. Phenology, in short, is a "horizontal science" which transects all ordinary biological professions. Whoever sees the land as a whole is likely to have an interest in it.

Phenology is more ancient than the "vertical" categories which it transects; its first paper, published about 974 B.C., cuts across three sciences, then not yet born: meteorology, botany, and ornithology:

For, lo, the winter is past,
The rain is over and gone:
The flowers appear on the earth;
The time of the singing of birds is come
And the voice of the turtle is heard in our land.
(Solomon, 2:12)

PURPOSE

The purpose of this paper is to assemble a composite phenological record for the wild plants, birds, and mammals of the region, with at least a sprinkling of items relating to other animals, waters, crop plants, and plants used in landscaping.

Such a record is useful for two main purposes. First, it permits one to interpolate, for any given event or any given date, a background of contemporaneous events. For example: a game manager learns from the literature that in Dane County the most frequent date of first egg-laying in pheasant is May 6. What else of possible importance to nesting pheasants is going on at that time? A glance at Tables 4 and 5 shows that spring grain [63] has been seeded two weeks ago and should be well up on May 6; that Franklin ground squirrel² [91] has already emerged; that bluegrass [142] will head out in eight days; that alfalfa hayfields [200] will be ready to cut in 38 days, which just about equals the time necessary to complete the clutch (12 days) and incubate it (21-24 days).

The second main purpose of a phenology table is to permit one to correct for early or late seasons by translating calendar dates into phenological "dates." Assume, for example, that the same game manager needs to find some pheasant nests, but that the season is very early, hence the average date of May 6 is invalid. How much earlier shall his search begin? A glance at Table 5 shows the following contemporaneous first blooms: sugar maple, chokecherry, winter cress, lousewort, white trillium, Jacob's ladder.

² Scientific names of the animals and plants referred to in the text are given after the common names in the phenology tables. Numbers in brackets are serial numbers in the phenology tables.

¹ Journal Paper No. 8 of the University of Wisconsin Arboretum.

Lilac has been blooming three days, wild crab will bloom in three days. With these "cross shots" on his problem, the vegetation will tell him in any year, early or late, about when to begin his search.

It is strangely difficult to arrive at such correlations by comparing specialized publications. To facilitate them, we have merged all of our events—plants, birds, mammals, insects, and weather—in one common sequence (Tables 1-12).

It is not to be assumed, of course, that the sequence of averages repeats itself exactly each year, and still less that the average sequence for our region is identical with that for other regions. Indeed the whole concept of a sequence of average dates is in one sense an abstraction, for it *can never be found in toto* in the field. Nevertheless it exists, and it is an important characteristic of the flora and fauna. The reasons for this will appear later.

SCOPE

No attempt is made in this paper to derive the correlations which are its principal purpose. They are so numerous that the reader can best derive them for himself, if and when needed. An attempt is made to suggest how to select items for phenological recording, and to deduce some responses of animals and plants to weather.

It is unnecessary for a phenologist to record as many species as are given in this paper. A smaller number, well assorted as to site and season, would be equally valuable.

Our arrival dates of migratory birds are confined largely to a few common, easily recognized species. Complete lists of average arrival dates for the Dane Station have been published by Schorger (1929, 1931), and for southern Wisconsin by Barger *et al* (1942).

The phenology of birdsong is largely omitted, and will be covered in a separate paper. The phenology of leaf-fall is omitted because it is difficult to define sharply, and there is excessive variability between trees.

References to the literature cover only the region studied, plus a few nationally-known papers that have influenced our work. The writers are aware that there is a large European literature, and that many important American papers are not mentioned.

STATIONS

This paper records some 328 events at two stations, herein called "Sauk" and "Dane." The first includes two or three square miles around the Leopold shack in Sec. 33, T. 13N, R. 6E, Sauk County. The second is an area of similar size including the University of Wisconsin Arboretum, and adjoining parts of the city of Madison and University of Wisconsin campus, in Dane County. The Dane station is 33 miles south and nine miles east of the Sauk station.

In a few instances, a scattered date from outside one or the other station has been included in it without specifying the exact point of origin. Such dates are considered eligible only when they fall within the following geographic limits:

	East to West	North to South
Sauk Station.....	Portage to Wisconsin Dells (20 miles)	Summit of Baraboo Hills to Wisconsin River (10 miles)
Dane Station.....	Faville Grove (Jefferson Co.) to Prairie du Sac. (40 miles)	Poynette to south line of County (30 miles)

Whenever all of the dates for any item originated elsewhere than Madison or the Leopold shack, their point of origin is specified.

Climate. The following comparison of the two

stations is taken mainly from "Climate and Man" (Anonymous 1941), and is based on 17 and 40 years' records, respectively.

TEMPERATURES

	Sauk (Wis. Dells Station)	Dane (Madison Station)	Sauk is:
Mean annual.....	44°-45°F.	45°-46°F.	1 degree colder
January average.....	16.0°F.	16.7°F.	0.7 degree colder
July average.....	71.6°F.	72.1°F.	0.5 degree colder
FROSTS, GROWING SEASON			
Last frost in spring.....	May 11	April 29	12 days later
First frost in fall.....	Sept. 27	October 17	20 days earlier
Growing season.....	139 days	171 days	32 days shorter
PRECIPITATION			
Average annual.....	30.78 ins.	30.60 ins.	0.18 inches wetter

The only large difference disclosed in these data is in the length of the frostless period or growing season, which is 32 days shorter at the Sauk station.

During the decade here reported (1935-1945) the growing season at Sauk was only 13 days shorter [see items 79 and 323 of Tables 1-12].

LIFE ZONES

No attempt will be made to describe our stations in terms of the biotic provinces proposed by various conflicting authors (Merriam *et al.*, 1928; Weaver & Clements, 1938). Both stations lie in the general region of confluence of prairie, oak-hickory forest, and coniferous forest. The first two categories are represented within the area of both stations; the third occurs only within the area of the Sauk station. The Sauk station exhibits certain southern species like red birch, red bellied woodpecker and prothonotary warbler, but it also exhibits certain northern species such as red squirrel and the three native pines. All of these species are absent, or only casual, at the Dane station.

ELEVATIONS

Lake Mendota at Madison is 849 feet above sea-level; the Wisconsin River at Wisconsin Dells is 815 feet. The more southerly station is thus 34 feet higher.

LAND USE

The Sauk station and that part of the Dane station comprising the University Arboretum are alike in that both consist of reverted farms on which old fields, woods, and marshes are interspersed. Both are surrounded by active farms. The remainder of the Dane station is suburban.

SOILS

The soils of the Sauk station are Coloma sands and Dunning sands, with local traces of red clay from the bottom of glacial Lake Wisconsin. All lowlands have been reworked by river action. The soils of the Dane station are Miami silt loam and peat, the latter underlain by marl. (Whitson, 1927.)

WATERS

The Sauk station lies on the south bank of the Wisconsin River and its lowlands are flooded yearly. It has few springs and only small lakes. The Dane station has many springs, several large lakes, and no rivers. Its lowlands are never flooded.

WILDLIFE

The Sauk area is wilder, retaining deer, ruffed grouse, pileated woodpecker, and a few otters and prairie chickens. These species are absent from the Dane station.

OBSERVERS

This paper embodies three main blocks of phenological data:

1. A. Carl Leopold, plants and animals of the Sauk Station, 1935-1940.³
2. Sara E. Jones, plants of the University Arboretum, Dane Station, 1944-1945.

³ Leopold, A. Carl. 1940. Phenology table for Fairfield Township, Sauk County, Wisconsin, 1935-1940. Unpub. Ms., Dept. Wildlife Management, Univ. Wis., 30 pp.

3. Aldo Leopold, plants and animals of the Sauk Station, 1935-1945.

All of the Sauk dates, and a majority of the Dane dates, were taken by these observers. The remaining dates for the Dane station have been generously contributed by the following collaborators:

Name	Kinds of Items	What Part of Dane Station	Years	Reference if published
Anderson, Harry G., <i>et al.</i>	Birds, plants, mammals	Arboretum	1935-1939	(1942) ⁴
Barger, Norval R., <i>et al.</i>	Bird arrivals	Dane County	1935-1945	(1942)
Buss, Irven O.	Birds, plants, mammals	Faville Grove	1937-1942	
Buss, Irven O. and Arthur S. Hawkins	Upland plover	Faville Grove	1935-1943	(1939)
Curtis, John T.	Spring plants	Dane County	1941-1942	
Feeney, W. S.	Birds, mammals	Arboretum	1938-1939	(1942)
Gastrow, Albert	Horned owl, skunk	Prairie du Sac	1935-1945	
Hale, James B.	Bird arrivals	Stoughton	1939-1945	
Hawkins, Arthur S.	Birds, mammals, plants	Faville Grove	1935-1938	
Jackson, Arnold S.	Bird arrivals	Dane County	1936-1942	
Koehler, Mrs. Arthur	Bird arrivals	Dane County	1936-1944	
Kumlien Ornithological Club	Bird arrivals	Dane County	1935-1945	
McCabe, Robert A.	Birds, mammals, plants	Arboretum	1943-1945	
Robbins, Samuel D., Jr.	Bird arrivals	Dane County	1940-1943	
Shands, H. H.	Grain and hay crops	University Farms at Madison	1935-1945	
Sowls, Lyle K.	Birds, mammals, plants	Faville Grove	1938	
Sperry, Theodore M.	Bird arrivals, plants	Arboretum	1938	(1942) ⁵
Thompson, Donald R.	Plants	Arboretum vs. City	1946	
Zimmerman, James	Plants, birds, mammals	Dane County	1944-1945	

PHENOLOGICAL TABLES

In the basic tables, in which the 328 events are assembled by months, each month bears its calendar number, beginning with Table 1 and 2 for January and February.

Each event on which dates are available is called an item, and each item bears a serial number (at the left), and an average date (at the right). Dates for both stations are given when available. When an event has a definite duration (such as the bloom of a plant), a double date indicates the duration. Few durations were recorded during the first three years of the decade.

The items are arranged chronologically, in order of the average date for the Sauk station.

⁴ Also: Anderson, Harry G. 1936. Avifauna of the University of Wisconsin Arboretum. Bachelor's thesis, Ms., Dept. Zoology, Univ. Wis., 166.

⁵ Also: Sperry, Theodore M. Artificial establishment of a tall-grass prairie on the University of Wisconsin Arboretum. Ms., pending publication.

TABLES 1-2. Phenology for January-February.

Species, Station, Item	1935	1936	1937	1938	1939	1940	1941	1942	1943	1944	1945	Average
1 SKUNK (<i>Mephitis mephitis</i>) Emerges from hibernation. (From Journal of Albert Gastrow.)												
Prairie du Sac:	2/27	2/22	2/14	3/4	1/21	2/15	2/7	1/11	1/24	2/14	2/9
2 GREAT HORNED OWL (<i>Bubo virginianus virginianus</i>) First egg (or first seen incubating).												
Dane:	1/25	3/11	2/13	2/24	2/18	2/16	2/20	2/6	2/16
Mostly from journal of Albert Gastrow, Prairie du Sac, Wis. In 1937, 1940, 1944, and 1945 no nesting occurred in the area, though the usual number of owls was present. See Errington (7) p. 6.												
3 CARDINAL (<i>Richmondia cardinalis cardinalis</i>) First song.												
Sauk:	2/4	3/23	(by 3/1)	2/28	3/13	2/26	2/8	2/27
Dane:	2/12	1/28	1/18	(by 3/17?)	1/30	2/16	1/20	1/24	1/13	1/14	1/26

TABLE 3. Phenology for March.

4 PHEASANT (<i>Phasianus colchicus torquatus</i>) First crowing.												
Sauk:	3/19	(by 3/31)	(by 3/30)	3/1	2/28	after (3/13)	2/26	3/8	3/5
Dane:	2/15	3/5	3/5	(by 3/21)	2/20	1/28	2/12	1/8	1/6	2/8
5 MARSHHAWK (<i>Circus hudsonius</i>) Migrants arrive.												
Sauk:	3/14	3/18	3/30	2/9	4/25	2/27	2/6	2/3	3/6
Dane:	3/6	3/1	2/25	2/11	3/4	3/17	3/14	3/8	3/20	3/2	3/8	3/5
6 WOODCHUCK (<i>Marmota monax</i>) Emerges from hibernation.												
Dane:	3/17	3/14	3/4	3/28	3/15	2/4	2/28	3/9	3/8
7 BLUEBIRD (<i>Sialia sialis sialis</i>) Arrives.												
Sauk:	3/14	3/6	3/11	(by 3/18)	(by 3/30)	3/29	3/14	3/5	3/10	3/7	3/12
Dane:	3/6	3/4	3/6	2/28	3/4	3/19	3/20	3/6	3/14	3/17	3/3	3/9
8 GRAY CHIPMUNK (<i>Tamias striatus griseus</i>) Emerges from hibernation.												
Dane:	3/13	3/18	3/13	3/19	3/14	3/31	3/3	3/16	3/16
9 EASTERN MEADOWLARK (<i>Sturnella magna magna</i>) Migrants arrive.												
Sauk:	3/14	3/19	3/10	3/23	3/21	(by 4/13)	(by 4/8)	(by 3/23)	3/17
Dane:	3/11	3/21	3/20	3/1	3/3	3/17	3/1	3/6	3/13	3/14	3/10	3/11
10 REDWINGED BLACKBIRD (<i>Agelaius phoeniceus artoleus</i>) Migrant males arrive.												
Sauk:	3/14	(by 3/18)	(by 3/30)	3/23	3/21	(by 4/2)	3/12	(by 3/23)	3/18
Dane:	2/23	2/29	3/6	3/2	3/3	3/17	3/2	2/5	2/23	2/26	3/4	2/28
11 BRONZE GRACKLE (<i>Quiscalus quiscula aeneus</i>) Arrives.												
Dane:	3/16	3/21	3/28	3/20	3/10	3/17	3/20	3/13	3/7	3/25	3/8	3/18
12 ROBIN (<i>Turdus migratorius migratorius</i>) Migrants arrive.												
Sauk:	3/14	3/11	(by 3/30)	3/23	(by 3/21)	(by 3/23)	(3/19)
Dane:	3/12	3/4	3/6	3/9	3/13	3/3	3/10	3/6	3/15	3/2	3/2	3/7
13 PRAIRIE MOLE (<i>Scalopus aquaticus macrinus</i>) Active runs on surface.												
Sauk & Dane:	3/25	4/6	4/6	3/13	2/27	(by 4/8)	3/13	3/21
14 WISCONSIN RIVER (in Fairfield Township, Sauk County)												
Ice breaks:	3/21	3/28	3/19	3/18	3/31	3/31	3/10	3/27	3/10	3/21
In flood:	(by 3/29)	3/30	(by 3/27)	(by 3/31)	none	3/29	none	3/20	(3/26)
15 KILDEER (<i>Oryzopsis vociferus vociferus</i>) Arrives.												
Sauk:	4/6	3/6	(by 4/9)	(3/21)
Dane:	3/14	3/7	3/6	3/9	3/3	3/17	3/19	2/5	2/23	3/23	2/24	3/6
16 CANADA GOOSE (<i>Branta canadensis</i>) Arrives.												
Sauk:	3/21	3/24	3/11	3/31	3/30	3/29	3/7	4/3	3/11	(by 3/23)	3/21
Dane:	3/14	3/12	3/25	3/9	2/26	3/9	2/25	3/6	3/21	3/24	3/4	3/11
17 EASTERN MOURNING DOVE (<i>Zenaidura macroura carolinensis</i>) Migrants arrive.												
Sauk:	3/10	4/3	(by 4/10)	(by 4/8)	3/24	(3/23)
Dane:	3/16	3/12	3/19	3/18	3/21	3/21	3/23	2/21	3/24	3/24	3/11	3/17
18 WOODCOCK (<i>Philohela minor</i>) Arrives.												
Sauk:	3/11	3/25	3/30	4/5	3/21	4/4	(by 4/8)	3/15	3/25
Dane:	3/16	3/18	4/1	3/11	3/24	3/29	3/27	3/3	4/1	3/17	3/21
19 FOX SPARROW (<i>Passerella iliaca iliaca</i>) Arrives.												
Sauk:	3/19	3/27	(by 4/18)	4/5	(by 4/2)	3/23	3/26
Dane:	3/15	3/14	3/28	3/16	3/18	3/29	3/23	3/25	3/22	3/29	3/15	3/21
20 LEOPARD FROG (<i>Rana pipiens</i>) First seen on land.												
Sauk & Dane:	3/23	3/21	4/7	3/19	3/23	4/5	3/31	3/23	3/26
21 SPRING CANKERWORM (<i>Paleacrita vernata</i>) Adult moths ascend trees.												
Sauk:	4/6-7	3/30-4/19	3/21-7	3/25-4/9	7-4/23	3/23-4/1	3/27

Ascent is detected by trapping in rings of tanglefoot. Caterpillars descend to pupate during May.

Species, Station, Item	1935	1936	1937	1938	1939	1940	1941	1942	1943	1944	1945	Average
22 LAKE WINGRA at Madison. Ice breaks.												
	3/25	3/24	4/10	3/21	3/25	4/9	3/24	3/17	3/27
23 BROWN BAT (<i>Myotis lucifugus lucifugus</i>) Flying.												
Dane:.....	4/15	4/22	3/14	3/17	3/30	3/14	3/29
24 EARTHWORM (<i>Lumbricus terrestris</i>) On surface of ground.												
Dane:.....	4/18	4/6	3/27	(by 4/18)	3/4	3/29
25 CRICKET FROG (<i>Rana palustris</i>) First heard calling.												
Sauk:.....	3/30	3/20	3/25	(by 3/30)	3/29	3/31	3/31	4/7	3/29
Dane:.....	3/20	3/18	4/1	3/23	3/30	3/21	(by 3/15)	3/24

A live specimen taken at Prairie du Sac March 31, 1943, was identified as this species. It is believed the entire record is for cricket frogs, but in any event it represents the first audible small frog.

TABLE 4. Phenology for April.

26 SILVER MAPLE (<i>Acer saccharinum</i>)												
Sauk:												
flower buds open	3/20	3/25	4/10	4/12	4/3	4/1	4/8	3/24	4/1
ripe samaras fall	5/20-6/3	6/8-?	7-5/23	5/20-5/25	5/29-?	(by 5/27)	5/18-?	5/25
Dane:												
in pollen (b)	4/14-?	3/20-?	3/25-?	4/10-?	3/22-?	4/1-4/20	4/16-4/23	3/17-3/26	3/31
staminate flowers fall	4/27	3/25	(4/11)
ripe samaras fall	5/15-6/1	(5/15)
In 1945 leafing began at the end of blooming and was completed a month later. In 1944 leafing began a week after the end of bloom and was completed in 17 days.												
27 LAKE MENDOTA at Madison.												
Ice breaks:	3/28	3/30	4/13	3/22	4/4	4/16	4/9	3/24	3/31	3/29	3/20	4/1
The average date for the period 1853-1940 was April 6. See Wing, page 158.												
28 SKUNK CABBAGE (<i>Symplocarpus foetidus</i>)												
Sauk: in pollen	4/16	3/30	3/20	(4/1)
29 STRIPED SPERMOPHILE (<i>Citellus tridecemlineatus tridecemlineatus</i>) Emerges.												
Dane:.....	4/2	4/8	4/10	3/28	4/23	3/30	3/12	4/3	4/13	3/26	4/3
30 YELLOW-BELLIED SAPSUCKER (<i>Sphyrapicus varius varius</i>) Arrives.												
Sauk:.....	3/11	4/13	4/5	4/9	4/7	4/3
Dane:.....	4/4	3/24	4/4	3/30	4/8	4/1	4/4	3/26	3/30	4/2	3/28	4/1
31 GREAT BLUE HERON (<i>Ardea herodias herodias</i>) Arrives.												
Sauk:.....	(by 4/9)	3/25	4/6	4/19	4/2	4/5
Dane:.....	3/30	3/15	4/1	3/19	3/19	3/29	3/22	4/5	3/21	3/20	3/18	3/24
32 MOURNING CLOAK BUTTERFLY (<i>Aglais antiope</i>) First seen.												
Sauk & Dane:.....	3/26	4/15	4/18	3/22	3/25	4/16	4/12	(by 4/19)	4/8	3/23	4/5
33 COWBIRD (<i>Molothrus ater ater</i>) Arrives.												
Sauk:.....	4/20	3/30	4/12	4/9	3/23	4/6
Dane:.....	3/23	3/21	3/21	3/13	3/22	3/18	3/30	4/2	3/22	4/9	3/21	3/24
34 PUSSY WILLOW (<i>Salix discolor</i>)*												
Dane: in pollen (b)	3/25-?	3/30-?	4/6-?	4/16-?	4/18-?	4/17-4/30	3/24-4/3	4/6
35 WILSON SNIPES (<i>Capella delicata</i>) First migrants arrive.												
Sauk:.....	(by 4/19)	(by 4/17)	(by 4/17)	4/7	4/15	4/12	4/3	4/11	3/25	4/7
Dane:.....	3/23	2/29	3/27	3/11	3/20	3/26	3/27	4/4	4/8	3/28	3/23
36 FIELD SPARROW (<i>Spizella pusilla pusilla</i>) Arrives.												
Sauk:.....	4/17	3/27	4/7	4/15	4/12	4/12	4/3	4/7	3/23	4/7
Dane:.....	3/29	3/28	4/7	3/22	4/8	4/3	3/22	3/22	4/2	4/3	3/30	3/30
37 PHOEBE (<i>Sayornis phoebe</i>) Arrives.												
Sauk:.....	4/9	4/2	4/7	4/18	4/3	4/20	3/24	4/7
Dane:.....	3/23	3/14	4/2	3/21	3/24	4/2	4/7	3/29	4/2	4/9	3/17	3/28
38 HAZEL (<i>Corylus americana</i>)												
Sauk: in pollen	3/29-?	4/13-?	4/12-?	(by 4/3)	7-4/23	7-3/25	(4/7)
Dane: in pollen	3/25-?	4/11-?	3/31-?	4/9-?	4/9-4/23	3/18-3/26	4/2
The catkins fall about a week after they have ceased to bear pollen. In 1945 the leaf buds enlarged when the catkins fell, and the leaves attained full size a month and a half later.												
39 RUFFED GROUSE (<i>Bonasa umbellus umbellus</i>) Drums.												
Sauk:.....	(by 4/19)	3/29-?	3/27-?	4/16-?	4/14-6/2	4/5-6/14	4/12-6/16(5/31) only	4/8-7/3	4/7-6/16	4/8-6/16	
40 ALDER (<i>Alnus incana</i>)												
Sauk: in pollen	3/23-?	4/13-?	4/12-?	4/13-?	4/13-?	4/8-4/23	7-3/23	4/8
Dane: in pollen (b)	4/14-?	3/27-?	4/6-?	(by 4/18)	3/31-?	4/5-4/20	4/10-4/23	3/17-3/26	4/2

Species, Station, Item	1935	1936	1937	1938	1939	1940	1941	1942	1943	1944	1945	Average
41 QUAKING ASPEN (<i>Populus tremuloides</i>)												
Sauk & Dane:												
in pollen.....	4/20	4/21	4/14	4/2	4/11	3/23	4/10
This species is genetically variable in blooming, leafing, and fruiting dates. We could not relate these variations to site, but clones often displayed uniform phenology. The earliest seeds in 1945 blew on April 28. The earliest leafing was completed April 21.												
42 EASTERN BELTED KINGFISHER (<i>Megascery alcyon alcyon</i>) First migrants arrive.												
Sauk:.....	4/21	4/19	3/25	4/6	4/19	4/4	4/4	(by 4/8)	(by 3/29)	4/10
Dane:.....	3/24	4/4	3/23	3/14	3/11	3/30	4/6	3/20	3/26	3/30	3/16	3/24
43 FORSYTHIA (<i>Forsythia suspensa</i>)												
Dane: in bloom (b).....	4/20-?	(by 5/9)	4/16-?	4/12-?	4/18-5/17	3/24-4/18	4/10
44 PASQUE FLOWER (<i>Anemone patens</i> var. <i>Wolfgangiana</i>)												
Sauk: in bloom.....	(by 5/1)	?-5/12	4/28-5/26	?-5/3	4/12-5/1	4/11-5/10	4/10-5/15	3/24-4/16	4/11
Dane: in bloom.....	4/20-?	4/12-?	3/29-?	4/10-?	4/20-5/1	4/11-?	4/13-?	3/29-4/7	4/10
45 COTTONWOOD (<i>Populus deltoides</i>)												
Dane: staminate catkins in pollen.....	4/19-?	4/16-?	4/28-5/4	3/22-3/29	4/13
In 1945 the staminate flowers and flower scales fell March 28-29, immediately after the cessation of pollen. Leafing followed blooming. The earliest seeds blew on April 28, but seeds were still blowing up to June 18.												
46 AMERICAN ELM (<i>Ulmus americana</i>)												
Sauk:												
flower buds open....	4/19	4/19	4/10	3/23	4/10
flowers in pollen.....	4/26-5/4	?-4/20	4/15-?	4/20-?	3/26-?	4/14
fruit ripe and falling.....	5/11-6/1	(by 5/21)	5/18-?	?-6/3	(by 5/18)	(5/12)
Dane:												
flower buds open....	4/19	4/13	4/9	3/17	4/2
flowers in pollen.....	4/23-?	4/1-?	4/14-?	4/16-4/26	3/21-4/7	4/9
47 BOX ELDER (<i>Acer negundo</i>)												
Dane: in pollen.....	4/19-?	4/16-?	4/15-?	4/23-5/6	3/28-4/5	4/14
In 1945 the staminate flowers fell immediately after pollen ceased. Leafing begins with pollen and is completed in about 3 weeks.												
48 HEPATICA (<i>Hepatica acutiloba</i> and <i>H. americana</i>)												
Dane: in bloom.....	4/23-?	4/24-?	4/15-?	4/22-?	4/12-?	4/13-?	4/4-?	4/28-5/16	4/23-5/13	3/22-4/17	4/15
49 UPLAND PLOVER (<i>Bartramia longicauda</i>) Arrives. (Dates up to 1943 from Buss and Hawkins.)												
Jefferson:.....	4/14	4/19	4/14	4/13	4/22	4/19	4/13	4/13	4/17	4/18	4/16
50 DOUBLE CRESTED CORMORANT (<i>Phalacrocorax auritus auritus</i>)												
Sauk:.....	4/9	4/17	4/19	4/14	4/12	4/12	4/16	5/6	4/6	4/16
Dane:.....	3/30	3/28	4/28	4/19	4/21	3/29	4/21	4/17	4/14	4/10	4/12
51 DRABA (<i>Draba reptans</i>)												
Sauk: first bloom.....	4/19	4/18	4/29	3/31	4/17
52 RED CEDAR (<i>Juniperus virginiana</i>)												
Sauk: in pollen (b).....	4/23-?	4/28-?	3/31-4/7	(4/17)
53 DANDELION (<i>Taraxacum officinale</i>)												
Dane: in bloom.....	4/29-?	4/17-?	4/18-?	4/7-5/23	?-6/2	?-5/23	4/12-5/20	4/17
54 EASTERN HERMIT THRUSH (<i>Hylocichla guttata fazoni</i>) Arrives.												
Sauk:.....	4/19	4/16	4/18	(4/18)
Dane:.....	3/27	3/29	3/27	3/22	3/26	4/5	4/4	3/25	3/30	4/14	3/14	3/29
55 RED EYED TOWHEE (<i>Pipilo erythrophthalmus erythrophthalmus</i>) Arrives.												
Sauk:.....	3/29	4/20	4/28	4/18	5/1	4/12	4/18
Dane:.....	3/29	4/15	4/18	3/27	4/11	4/14	4/19	4/1	4/1	4/15	3/25	4/7
56 DUTCHMAN'S BREECHES (<i>Dicentra cucullaria</i>)												
Sauk: in bloom (b).....	?-5/16	?-5/11	4/22-?	4/18-5/9	4/23-5/15	4/25-5/15	3/31-4/23	4/18
Dane: in bloom.....	4/17-?	4/15-?	4/26-?	4/14-?	4/25-?	4/20-?	4/19-?	5/1-5/16	3/30-4/29	4/18
57 PURPLE MARTIN (<i>Progne subis subis</i>) Arrives.												
Sauk:.....	4/18	4/20	4/18	(by 5/1)	(4/19)
Dane:.....	3/31	4/4	4/8	4/7	3/24	3/31	4/1	3/25	3/24	4/6	3/29	3/31
58 PUSSYTOES (<i>Antennaria fallax</i>)*												
Sauk: first bloom.....	4/21	4/27	4/25	4/23	4/21	3/31	4/20
Dane: first bloom.....	4/20-?	4/26-?	4/11-5/15	(4/19)
59 HORSETAIL (<i>Equisetum arvense</i>)												
Dane: spores blowing.....	4/22-?	4/19-?	4/30-5/24	4/10-5/18	4/20
60 TOOTHWORT (<i>Dentaria laciniata</i>)												
Dane: in bloom.....	4/19-?	5/6-5/20	4/5-4/16	(4/20)
61 BLOODROOT (<i>Sanguinaria canadensis</i>)												
Sauk: in bloom (b).....	4/25-?	4/23-5/10	5/1-?	4/3-4/22	4/21
Dane: in bloom.....	4/25-?	4/22-?	4/14-?	4/20-?	4/13-?	4/12-?	4/8-5/11	4/18-5/15	3/26-4/14	4/14

Species, Station, Item	1935	1936	1937	1938	1939	1940	1941	1942	1943	1944	1945	Average
62 NORWAY MAPLE (<i>Acer platanoides</i>)												
Dane: in pollen.....	4/22-?	4/19-?	4/22-?	5/9-5/16	4/5-4/11	4/21
63 SPRING GRAIN (oats and barley) Planted at University Farms.												
Dane:.....	4/22	4/18	5/8	4/21	4/27	4/20	4/24	4/17	4/22	5/1	3/27	4/21
Data from Prof. H. L. Shands, Dept. of Agronomy, College of Agriculture.												
64 BROWN THRASHER (<i>Toxostoma rufum</i>) Arrives.												
Sauk:.....	4/19	4/16	4/28	4/19	4/25	5/1	(by 5/7)	4/16	4/22
Dane:.....	4/21	4/23	4/10	3/20	4/21	4/28	4/19	4/18	4/24	4/24	4/8	4/17
65 CABBAGE BUTTERFLY (<i>Pieridae</i> sp?) First seen.												
Sauk & Dane:.....	4/20	4/23	4/28	4/25	4/25	4/18	4/30	4/12	4/23
66 CAREX (<i>Carex pennsylvanica</i>)												
Sauk: in pollen (b).....	5/7-?	5/1-5/16	4/1-?	(4/23)
Dane: in pollen.....	4/14-?	4/19-?	5/1-5/30	4/2-4/20	4/17
67 EARLY CROWFOOT (<i>Ranunculus fascicularis</i>)												
Sauk & Dane: in bloom.....	5/1-?	5/2-?	(by 4/26)	4/25-?	4/20-?	4/21-?	7-5/28	4/6-5/24	4/23
68 AMERICAN BITTERN (<i>Bolarus lentiginosus</i>) Arrives.												
Sauk:.....	4/18	5/11	4/19	4/25	4/23	4/21	4/23	4/24
Dane:.....	4/10	4/19	4/5	4/9	4/9	5/8	4/6	4/18	3/30	3/25	5/3	4/13
69 SHEPHERD'S PURSE (<i>Capsella Bursa-pastoris</i>)												
Sauk: first bloom.....	5/28	4/18	4/23	5/7	5/13	4/8	4/24
70 BELLWORT (<i>Uvularia grandiflora</i>)												
Dane: in bloom.....	5/13-?	5/1-?	4/25-?	4/27-?	4/28-?	5/10-5/25	4/12-5/21	4/29
71 MARSH MARIGOLD (<i>Caltha palustris</i>)												
Sauk: in bloom.....	4/22-5/23	5/11-5/26	4/27-?	4/22-?	7-5/15	4/28
Dane: in bloom.....	4/25-?	4/20-?	4/12-?	4/25-?	5/3-?	4/24-?	4/21-?	4/25-?	4/28-5/23	4/29-5/30	4/9-5/20
72 JUNE BERRY (<i>Amelanchier canadensis</i>)*												
Sauk: in bloom (b).....	(by 5/8)	4/22-5/2	5/11-?	4/26-?	4/25-5/7	5/1-5/15	5/11-5/19	4/12-4/23	4/28
Dane: in bloom (b).....	4/15-?	4/25-?	4/28-5/23	5/9-5/19	4/10-5/4	4/23
The budding period as between years has varied from five days to two weeks, apparently depending on current weather. Leafing and blooming occurred simultaneously in 1945, the leaves being completed before the end of bloom.												
73 BOBWHITE (<i>Colinus virginianus virginianus</i>) First "bobwhite" call.												
Sauk:.....	(by 5/23)	(by 6/4)	(by 6/3)	4/21	5/2	4/25	5/29	4/25	4/12	4/29
Dane:.....	3/18	3/29	4/19	4/18	4/14	4/19	3/22	4/6
74 ARABIS (<i>Arabis lyrata</i>)												
Sauk: first bloom.....	5/15	4/22	5/6	4/11	4/29
Dane: first bloom.....	(by 4/28)	4/20	4/19	(by 4/20)	(4/20)
This species has no sharp terminal date. In 1945 straggling blooms occurred through July.												
75 WOOD ANEMONE (<i>Anemone quinquefolia</i> var. <i>interior</i>)												
Sauk: in bloom.....	(by 5/1)	5/11-?	4/25-?	4/25-5/16	5/5-5/30	5/7-5/23	4/12-5/18	4/29
Dane: in bloom.....	4/30-?	5/9-?	4/21-?	4/25-?	4/21-?	5/1-5/23	5/5-5/24	4/9-6/1	4/26
76 PRICKLY ASH (<i>Zanthoxylum americanum</i>)												
Sauk: first pollen.....	5/1	5/2	5/17	4/12	4/25	5/7	5/12	4/14	4/30
Leafing in 1944 began three days after first bloom, and was completed 16 days later.												

TABLE 5. Phenology for May.

77 HOUSE WREN (<i>Troglodytes aedon</i>) Arrives.												
Sauk:.....	(by 5/11)	5/2	5/1	(by 5/7)	5/1	(by 5/5)	(5/1)
Dane:.....	4/16	4/14	4/30	4/17	4/23	4/29	4/15	4/18	4/25	4/27	4/23	4/22
78 SMALL FLOWERED CROWFOOT (<i>Ranunculus abortivus</i>)												
Sauk: in bloom.....	5/17-?	4/14-?	(5/1)
Dane: in bloom.....	5/17-?	5/1-?	5/7-?	4/19-?	5/9-5/27	4/13-6/14	4/26
79 LAST KILLING FROST (Record by U. S. Weather Bureau.)												
Sauk:.....	5/23	4/16	4/16	4/12	5/2	5/4	4/25	4/20	5/1	5/6	6/4	5/1
Dane:.....	5/4	4/23	4/16	4/10	4/13	5/3	4/24	4/19	5/1	4/16	6/4	4/27
80 HOARY PUCCOON (<i>Lithospermum canescens</i>)												
Sauk: in bloom.....	5/1-?	5/12-6/13	4/23-5/23	5/1-6/4	5/7-6/4	5/14-6/3	4/12-6/6	5/1
Dane: in bloom (b).....	5/10-?	5/11-?	5/10-?	5/8-?	4/30-?	4/10-?	5/3
Straggling bloom occurred for a week to 10 days beyond the regular blooming period in each of the last three years.												
81 DOGTOOTH VIOLET (<i>Erythronium americanum</i> and <i>E. albidum</i>)												
Sauk: in bloom.....	7-5/8	5/1-?	5/5-?	7-5/16	4/29-?	7-5/5	(5/2)
Dane: in bloom.....	5/11-?	5/7-?	5/1-?	4/20-?	4/25-?	5/8-5/15	4/10-5/20	4/29

Species, Station, Item	1935	1936	1937	1938	1939	1940	1941	1942	1943	1944	1945	Average
82 BIRD-FOOT VIOLET (<i>Viola pedata</i> var. <i>lineariloba</i>)												
Sauk: in bloom.....	5/1-?	5/1-6/4	5/12-6/5	4/30-5/23	4/25-5/31	5/8-6/4	5/11-6/1	4/21-6/6	5/2
Dane: in bloom.....	5/2-?	5/9-?	5/10-?	5/8-?	4/25-?	4/11-6/21	5/1

A few autumn blooms were seen in Sauk County, Sept. 20, 1944.

83 ARABIS (<i>Arabis drummondii</i>)												
Sauk: in bloom.....	5/1-?	5/7-?	5/11-5/31	4/22-5/20	5/3
84 RIVER BIRCH (<i>Betula nigra</i>)												
Sauk: in bloom.....	5/11-5/17	7-5/9	5/15-5/21	4/13-?	(5/3)

Leafing began with blooming in 1944, and was completed by May 31.

85 SAND CHERRY (<i>Prunus pumila</i>)												
Sauk: in bloom (b).....	7-5/30	7-5/9	4/25-5/9	5/9-5/27	5/17-5/25	4/22-5/20	5/3

The leafing period coincides with the blooming period.

86 EASTERN KINGBIRD (<i>Tyrannus tyrannus</i>) Arrives.												
Sauk:.....	5/1	(by 5/14)	5/4	5/2	5/1	5/2	5/2	(by 5/11)	5/18	5/4
Dane:.....	5/6	5/3	4/17	4/21	4/30	5/5	4/25	4/29	5/6	5/7	5/12	5/1

87 NORTHERN CRESTED FLYCATCHER (<i>Myiarchus crinitus boreus</i>) Arrives.												
Sauk:.....	(by 5/14)	5/4	4/29	5/1	5/8	5/11	(by 5/18)	5/4	5/4
Dane:.....	5/11	5/2	4/17	5/2	5/6	5/11	4/21	5/3	5/3	5/13	5/3	5/3

88 OAKS (<i>Quercus velutina</i> ; <i>macrocarpa</i> ; <i>borealis</i> var. <i>maxima</i> ; <i>alba</i>)												
Sauk: in pollen
Black.....	7-5/9	5/13-?	4/25-?	(5/4)	
Burr.....	7-5/9	5/20-?	4/20-?	(5/5)	
Red.....	5/10-?	5/8-?	5/17-?	(5/12)	
White.....	5/23-?	(5/23)	
Dane: in pollen
Black.....	4/30-?	4/30-?	5/15-5/19	4/25-5/7	(5/3)	
Burr.....	5/15-5/19	4/20-4/30	(5/6)	

In general, black and burr oak bloom first; red and white later. In 1944, pollen developed in all species 4-6 days after the catkins appeared, whereas in 1945 about three weeks elapsed before pollen appeared. In both years leafing began with the first catkins, but completion of leafing required only 2 weeks in 1944, but over a month in 1945. In 1945 the catkins and young leaves of many oaks were destroyed by frost. Some such trees did not complete releafing until June.

89 STEMLESS BLUE VIOLET (<i>Viola cucullata</i>)*												
Dane: in bloom.....	5/2-?	5/9-?	5/11-?	5/13-?	5/13-6/1	4/6-5/31	5/4

90 BELLWORT (<i>Oakesia sessilifolia</i>)												
Sauk: first bloom.....	5/11	4/25	5/7	5/7	5/1	5/4

91 FRANKLIN GROUND SQUIRREL (<i>Citellus franklini</i>) Emerges.												
Dane:.....	5/4	4/21	5/12	5/10	5/4

92 WILD PLUM (<i>Prunus americana</i>)												
Sauk: in bloom.....	7-5/3	7-5/9	4/25-5/9	5/8-?	5/13-?	4/16-?	5/5
Dane: in bloom.....	5/2-?	4/12-4/29+	5/1-?	4/25-?	5/5-5/22	5/12-5/22	4/26-5/14	4/29
Sauk & Dane:
fruit ripe.....	8/25	8/29	8/25	(8/26)

Leafing begins with blooming, but is completed before the end of bloom.

93 GEUM (<i>Geum triflorum</i>)												
Sauk: in bloom (b).....	(by 5/2)	5/19-5/27	4/25-5/7	(5/5)
Dane:.....	4/28-?	5/1-6/14	(4/30)

94 PIN CHERRY (<i>Prunus pennsylvanica</i>)												
Sauk: in bloom.....	5/17	5/7	5/12	4/13	5/5
Dane: in bloom.....	5/8-?	5/11-?	5/7-?	7-5/17	4/10-4/29	5/1

95 BALTIMORE ORIOLE (<i>Icterus galbula</i>) Arrives.												
Sauk:.....	(by 5/10)	(by 5/14)	5/11	5/2	5/1	5/2	5/11	5/7	5/5
Dane:.....	5/7	5/2	5/7	5/2	5/4	5/5	4/29	4/29	5/1	5/2	5/6	5/3

96 EASTERN WARBLING VIREO (<i>Vireo gilvus gilvus</i>) Arrives.												
Sauk:.....	5/7	5/12	5/1	5/1	5/9	(by 5/12)	(by 5/18)	5/5
Dane:.....	5/8	5/3	5/8	4/30	5/4	5/12	5/1	5/1	5/2	5/5	5/8	5/5

97 SUGAR MAPLE (<i>Acer saccharum</i>)												
Dane: in pollen.....	5/11-?	5/25-?	5/8-5/16	4/7-?	5/5

98 BOBOLINK (<i>Dolichonyx oryzivorus</i>) Arrives.												
Sauk:.....	5/7	5/4	5/2	5/9	5/7	(by 5/18)	5/6	5/6
Dane:.....	4/25	5/2	4/26	5/4	5/3	5/5	5/4	4/29	5/9	5/13	5/9	5/3

99 ROSE BREASTED GROSBEEK (<i>Hedymeles ludovicianus</i>) Arrives.												
Sauk:.....	5/10	5/11	5/2	5/1	5/6	5/6
Dane:.....	5/7	5/1	5/9	5/1	5/6	5/6	5/7	5/1	5/8	5/6	5/9	5/6

Species, Station, Item	1935	1936	1937	1938	1939	1940	1941	1942	1943	1944	1945	Average
100 CHOKE CHERRY (<i>Prunus virginiana</i>)												
Sauk: in bloom.....	7-5/20	7-5/31	5/2-?	5/1-5/11	7-5/29	5/20-5/29	5/1-?	5/6
Dane: in bloom.....	5/8-?	5/11-?	5/4-?	4/27-?	5/21-?	5/18-6/3	4/27-5/23	5/8
Leafing is completed just before blooming begins. In 1944 leafing took 19 days in both Sauk and Dane. Flower buds became visible after leafing was one third completed. Fruit ripens at the end of August.												
101 WINTER CRESS (<i>Barbarea vulgaris</i>)												
Sauk: in bloom.....	5/20-?	4/21-6/6	(5/6)
Dane: in bloom.....	5/9-?	5/16-7/9	4/21-?	(5/8)
102 LOUSEWORT (<i>Pedicularis canadensis</i>)												
Sauk: in bloom.....	(by 5/17)	5/2-?	5/9-?	7-5-20	(5/6)
103 NORTHERN YELLOWTHROAT (<i>Geothlypis trichas brachidactyla</i>) Arrives.												
Sauk:.....	5/7	5/8	5/7	(by 5/17)	(5/7)
Dane:.....	4/27	5/1	5/5	5/2	5/5	5/6	5/1	4/30	4/24	4/30	4/26	5/1
104 WHITE TRILLIUM (<i>Trillium grandiflorum</i>)												
Sauk: in bloom.....	(by 5/1)	7-5/29	5/16-?	5/2-5/18	5/1-6/1	5/9-6/3	5/11-5/27	5/1-6/5	5/7
Dane: in bloom.....	5/12-?	5/3-?	5/6-?	4/26-5/23	5/6-?	5/7-5/25	4/15-5/26	5/3
105 CRATAEGUS*												
Sauk: (one plant)
in bloom (b.).....	(by 5/20)	5/1-?	7-5/31	5/19-5/27	5/1-5/20	(5/7)
Dane: in bloom.....	5/16-5/26	5/1-?	(5/9)
106 NORTHERN WOOD THRUSH (<i>Hylocichla mustelina</i>) Arrives.												
Sauk:.....	5/7	5/10	5/9	5/9	5/7	(by 5/17)	5/8
Dane:.....	5/8	5/2	4/17	4/30	5/6	4/13	5/4	5/1	5/5	5/5	4/12	4/28
107 BLUEBERRY (<i>Vaccinium pennsylvanicum</i>)												
Sauk: first bloom (b.).....	5/17	5/2	5/5	wind burn	no bloom	(5/8)
108 INDIAN SWEET GRASS (<i>Hierochloa odorata</i>)												
Sauk: in bloom.....	4/27-?	5/20-?	5/11-?	7-5/18	5/1-6/9	5/19-5/31	4/29-6/15	5/8
109 TRILLIUM (<i>Trillium recurvatum</i>)												
Dane: in bloom.....	5/12-?	5/11-?	5/5-?	5/16-6/1	4/29-5/27	5/8
110 WILD CRAB (<i>Pyrus ioensis</i>)												
Dane: in bloom.....	5/15-?	5/5-5/20	5/8-?	5/7-5/25	5/24-?	5/19-5/26	4/19-5/24	5/9
111 SCARLET TANAGER (<i>Piranga erythromelas</i>) Arrives.												
Dane:.....	5/8	5/6	(by 5/16)	5/7	5/14	5/12	5/2	5/16	4/30	5/1	5/21	5/9
112 EASTERN WHIPPOORWILL (<i>Antrostomus vociferus vociferus</i>) Arrives.												
Sauk:.....	5/17	5/9	5/8	5/6	(by 5/17)	5/10
Dane:.....	5/5	4/24	5/4	4/18	4/23	5/2	4/21	4/15	5/3	5/1	3/28	4/24
113 LILAC (<i>Syringa vulgaris</i>)												
Sauk: flower buds
visible.....	4/12	4/15	5/7	4/1	4/16
in bloom (b.).....	5/25-?	5/1-5/19	7-6/3	5/19-5/30	5/5-5/25	5/10
Dane:.....	4/28-5/25	5/4-5/30	4/30-5/23	5/20-?	5/16-5/28	4/12-5/16	5/3
The 1944 and 1945 record for Dane is for an early variety, S. V. Claude Bernard. Leafing begins 3-4 weeks before first bloom and is completed shortly after.												
114 PROTHONOTARY WARBLER (<i>Protonotaria citrea</i>) Arrives.												
Sauk:.....	5/12	5/9	(by 5/16)	5/14	5/12	(by 5/11)	5/16	5/8	absent	5/10
115 INDIGO BUNTING (<i>Passerina cyanea</i>) Arrives.												
Sauk:.....	5/4	5/9	(by 5/21)	5/20	(5/11)
Dane:.....	5/12	5/9	5/16	5/6	5/6	5/10	5/5	5/8	5/5	5/17	5/14	5/10
116 BLUE PHLOX (<i>Phlox divaricata</i>)												
Sauk: in bloom.....	5/26-6/13	5/9-6/7	5/1-6/4	5/13-6/15	7-6/15	5/5-6/10	5/11
Dane: in bloom.....	5/27-?	5/17-?	5/15-?	5/15-?	4/28-?	5/12-6/1	4/29-5/20	5/12
117 JACK PINE (<i>Pinus Banksiana</i>)												
Sauk: in pollen.....	5/30-?	5/2-?	5/1-5/13	5/18-5/25	5/6-5/15	5/11
118 JACK IN THE PULPIT (<i>Arisaema triphyllum</i>)												
Dane: in bloom.....	5/23-?	5/12-?	4/27-?	5/9-?	5/20-6/1	5/15-6/4	5/11
119 JACOB'S LADDER (<i>Polemonium reptans</i>)												
Sauk: in bloom (b.).....	5/13-5/31	5/19-5/29	5/5-5/25	(5/12)
Dane: in bloom.....	5/1-?	5/11-?	4/28-?	5/22-?	5/14-5/31	4/14-5/18	5/5
120 WILD STRAWBERRY (<i>Fragaria virginiana</i>)												
Sauk: in bloom.....	5/18-?	5/16-?	5/20-?	4/23-6/8	5/12
fruit ripe.....	6/1-6/13	6/17-?	6/17-7/3	(6/11)
Dane: in bloom.....	5/21-?	5/8-?	5/10-?	5/16-?	5/7-?	4/30-?	5/17-?	4/14-6/15	5/8
121 RED OZIER DOGWOOD (<i>Cornus stolonifera</i>)												
Dane: in bloom.....	5/14-?	5/7-?	5/22-6/2+	5/7-6/6+	5/12

Species, Station, Item	1935	1936	1937	1938	1939	1940	1941	1942	1943	1944	1945	Average
122 CATBIRD (<i>Dumetella carolinensis</i>) Arrives.												
Sauk:.....								5/16	5/9	(by 5/13)	(by 5/18)	(5/13)
Dane:.....	5/6	5/2	5/4	4/15	5/5	5/6	4/27	4/30	5/8	5/2	5/8	5/2
123 ASIATIC HONEYSUCKLE (<i>Lonicera tatarica</i>)												
Dane: in bloom.....								5/11-?	5/27-?	5/16-5/27	4/29-6/1	5/13
124 EASTERN NIGHTHAWK (<i>Chordeiles minor minor</i>) Arrives.												
Sauk:.....								5/16	5/7	(by 5/13)	(by 5/18)	(5/14)
Dane:.....	5/12	5/7	5/1	5/4	4/19	5/12	5/3	5/4	5/4	5/11	5/20	5/6
125 FALSE SOLOMON'S SEAL (<i>Smilacina stellata</i>)												
Sauk: in bloom.....						5/17-6/3	5/23-?	5/9-6/2	5/21-6/5	5/19-5/31	5/7-?	5/16
Dane: in bloom.....			5/22-?					4/30-?	5/17-?	5/16-5/27	4/28-5/27	5/11
126 WILD CHERRY (<i>Prunus serotina</i>)												
Sauk: in bloom.....						5/17-?		5/1-?	5/30-6/6			(5/16)
Dane: in bloom.....		5/15-?	5/18-?	5/10-?						5/26-6/8	5/19-6/5	5/14
127 WOOD SORREL (<i>Oxalis violacea</i>)												
Sauk: in bloom.....						5/19-6/1	5/9-?	(by 5/13)	5/30-?	5/20-6/5	5/5-6/17	5/17
Dane: in bloom.....			5/15-?		(by 5/29)		5/8-?	4/30-?	5/22-?	5/22-6/12	5/14-6/16	5/13
128 VIRGINIA WATERLEAF (<i>Hydrophyllum virginianum</i>)												
Dane: in bloom.....							5/20-?	5/13-?		5/19-6/15	5/17-6/22	5/17
129 COLUMBINE (<i>Aquilegia canadensis</i>)												
Sauk: in bloom.....					(by 5/19)	6/1-?	5/9-6/11	5/9-6/23+	5/25-6/14+	5/22-6/13+	5/18-6/28	5/19
Dane: in bloom.....		5/17-?	5/20-?	5/22-?	5/20-?		5/13-?	5/13-?	5/17-?	5/22-?	5/17-6/30	5/18
130 BLUE-EYED GRASS (<i>Sisyrinchium campestre</i>)*												
Sauk: in bloom.....					5/20-?	5/26-?	?-5/23	5/9-?	5/25-6/5	5/22-?	5/13-6/17	5/19
Dane: in bloom.....				5/26-?			5/12-?		5/30-?		5/15-7/6	5/21
131 LUPINE (<i>Lupinus perennis</i>)												
Sauk: in bloom.....							5/9-5/29	5/17-6/7	5/28-6/17	5/25-6/17	5/21-7/4	5/20
seed pods ripe, opening.....							6/21-6/25	6/21-6/25	6/25-?	7/1-7/4	7/8-7/?	6/27
Dane: in bloom.....							5/24-?	5/31-?		5/25-6/28	5/21-6/24	5/25
seed pods ripe, opening.....											7/6-7/17	(7/6)
On July 8, 1945, on the University Arboretum about 2:30 P.M. a large patch of lupine was ripening its pods and projecting the seeds. The sound of popping pods could be heard while approaching the patch, and the projected seeds could be seen flying through the air to a distance of a yard from the parent plant.												
132 GOLDEN ALEXANDER (<i>Zizia aurea</i>)												
Dane: in bloom.....								5/9-?		5/20-6/17	5/30-6/27	(5/20)
133 SPIRAEA (<i>Spiraea van Houttei</i>)												
Dane: in bloom.....							5/16-?	5/13-?	6/1-6/19	5/24-6/4+	5/16-6/12	5/20
134 BASTARD TOADFLAX (<i>Comandra Richardsiana</i>)												
Sauk: in bloom.....						5/25-?		5/9-?	5/31-?	5/20-6/5	5/19-?	5/21
Dane: in bloom.....							5/8-?	4/30-?			5/15-6/27	(5/8)
135 WILD GERANIUM (<i>Geranium maculatum</i>)												
Sauk: in bloom.....						6/1-?		5/9-6/13	5/23-6/16	5/21-6/15	5/18-6/17	5/21
Dane: in bloom.....	5/20-?		5/18-?	5/3-?			5/7-?	5/2-?	5/9-?	5/15-?	5/7-6/22	5/10
136 TOADFLAX (<i>Linaria canadensis</i>)												
Sauk: in bloom.....			?-6/6	5/20-?	(by 5/20)	5/26-?	5/23-6/25	5/9-6/21	5/27-6/20	5/29-6/15	5/20-6/30	5/22
Dane: in bloom.....							5/17-?	5/9-?			(by 5/25-6/22)	(5/13)
137 SHOOTING STAR (<i>Dodecatheon Meadia</i>)												
Sauk: in bloom.....						5/26-?	(by 5/22)	5/9-?	5/25-?	5/27-?	5/23-6/15	5/22
Dane: in bloom.....		5/18-?	5/20-?	5/14-?			5/13-?	5/9-?		5/19-6/10	5/7-6/24	5/14
138 YELLOW WOOD SORREL (<i>Oxalis stricta</i> var. <i>pulegioides</i>)												
Sauk: in bloom.....								5/22-8/13	6/2-8/13	6/11-8/5	4/21-?	5/22
Dane: in bloom.....			5/18-?			5/23-?				6/1-?	5/25-?	5/24
139 TALL YELLOW LADY'S SLIPPER (<i>Cypripedium parviflorum</i> var. <i>pubescens</i>)												
Dane: in bloom.....				5/21-?			5/13-?		5/29-6/19	5/22-6/6	5/23-6/2	5/22
140 MULBERRY (<i>Morus alba</i>)												
Dane: in bloom.....										5/21-5/26	5/22-5/29	(5/22)
fruit ripe.....				6/15-?					7/1-?	6/25-7/20	6/26-?	6/24
141 PUCCOON (<i>Lithospermum angustifolium</i>)												
Dane: in bloom.....							5/19-?			5/19-7/2	6/1-6/20	(5/23)

Species, Station, Item	1935	1936	1937	1938	1939	1940	1941	1942	1943	1944	1945	Average
142 KENTUCKY BLUEGRASS (<i>Poa pratensis</i>)												
Sauk: first lawn mowed	5/2	5/1	5/7	5/6	4/14	4/30
in bud (headed)	5/22	5/20	5/1	5/13	5/5	5/12
in pollen	5/18	5/29	5/25	6/8	(5/24)
Dane: first lawn mowed	5/1	4/11	(4/21)
in bud (headed)	5/15	5/16	5/20	5/18	5/1	5/14
143 PINK PHLOX (<i>Phlox pilosa</i> var. <i>fulgida</i>)												
Sauk: in bloom	7-6/17	5/26-7	5/25-6/12	5/23-6/11	5/31-7	7-6/13	6/1-6/30	5/26
Dane: in bloom	5/28-7/8	5/29-7	5/13-7	5/2-7	5/30-6/18	5/12-7/16	5/19
144 MANDRAKE (<i>Podophyllum peltatum</i>)												
Sauk: in bloom	5/16-7	6/4-7	7-5/27	frozen	(5/26)
Dane: in bloom	6/1-7	5/18-7	5/13-7	5/14-7	5/30-7	(by 5/26-7)	frozen	5/21
145 NANNYBERRY (<i>Viburnum Lentago</i>)												
Sauk: in bud	5/2	5/8	5/13	4/21	5/4
in bloom	6/1-7	5/18-7	5/23-5/31	5/30-7	5/25-6/2	5/26
Leafing: In 1944 leafing began 13 days before the flower-buds appeared, and was completed a week later, and 5 days before first bloom.												
146 SHEEP SORREL (<i>Rumex acetosella</i>)												
Sauk: in bloom	5/19-7	(by 5/30)	5/25-7	5/30-7	5/25-7/2	5/29-6/25	5/30-7	6/1-7	5/27
Dane: in bloom	5/17-7	4/30-7	5/15-6/28	(5/11)
147 YELLOW STAR GRASS (<i>Hypoxis hirsuta</i>)												
Sauk: in bloom	5/26-7	5/23-7	5/30-6/22	5/30-6/13	6/10-7	5/27
Dane: in bloom	5/26-7	(by 5/30)	5/29-7	6/6-7/10	(5/31)
148 WILD GRAPE (<i>Vitis vulpina</i>)												
Sauk: in bloom	(by 6/6)	5/23-6/8	5/23-7	5/23-6/3	7-6/17	5/30-6/7	6/5-7	5/27
fruit ripe	8/29	8/21	8/27	9/3	none	8/27
Dane: in bloom	5/30-6/5	6/2-6/20	(6/1)
149 GOLDEN RAGWORT (<i>Senecio aureus</i>)*												
Sauk: in bloom	(by 5/29)	5/30-7	5/21-6/5	6/1-6/17	5/28
Dane: in bloom	5/11-7	5/5-7	5/18-6/7	5/13-6/23	(5/14)
150 BLACK RASPBERRY (<i>Rubus occidentalis</i>)												
Sauk: in bloom	5/23-5/30	6/1-7	5/30-7	(5/28)
fruit ripe	7/2-7	7/1-7	6/25-7/12	7/5-7/25	7/3-7/15	7/18-7/30	7/4
Dane: in bloom	5/28-6/11	5/18-6/15	(5/23)
fruit ripe	7/1-7/15	7/4-7/18	(7/2)
151 CINQUEFOIL (<i>Potentilla simplex</i> var. <i>typica</i>)												
Sauk: in bloom	5/23-7	5/31-7	5/26-6/25	6/1-7	5/28
Dane: in bloom	6/5-7	5/29-7	5/30-7	(5/31)
152 SHAGBARK HICKORY (<i>Carya ovata</i>)												
Dane: in pollen	5/27-7	5/25-7	5/23-5/28	6/9-6/14	5/29
The catkins appear with the leaves, but are not in pollen until leafing is completed.												
153 BLACKBERRY (<i>Rubus allegheniensis</i>)*												
Sauk: in bloom	5/25-6/11	6/8-7	5/23-5/31	5/26-6/7	6/1-6/17	5/29-6/15	6/1-6/30	5/30
fruit ripe	7/23-7	8/1-8/31	8/1-8/29	7-8/25	7-8/10	7/26-9/5	7-8/21	7/20-9/4	8/17-9/5	7/30
Dane: in bloom	5/27-7	5/23-7	5/28-6/11	5/18-6/16	5/24
fruit ripe	8/5-7	7-8/29	7/23-8/20	8/10-9/12	(8/2)

TABLE 6. Phenology for June.

154 PUCCOON (<i>Lithospermum carolinense</i>)												
Sauk: in bloom	6/13-7	5/18-6/30	5/23-6/21	6/14-7	6/1-7/1	6/1-6/15	6/1
Dane: in bloom	5/17-7	5/20-7/2	5/19-7/20	(5/19)
155 WILD ROSE (<i>Rosa blanda</i> var. <i>hispida</i>)												
Sauk: in bloom	(by 6/4)	5/27-6/17	6/9-7	5/18-6/14	5/23-6/25	6/4-6/25	5/29-6/26	6/13-7/14	6/1
Dane: in bloom	6/1-7	6/3-7	5/31-7	6/2-7/20	6/1
156 VETCH (<i>Vicia angustifolia</i>)												
Sauk: in bloom	6/1-7/4	5/30-7/4	(by 6/15)	(6/1)
Dane: in bloom	6/6-8/20	6/11-7/7	(6/9)
157 ANEMONE (<i>Anemone cylindrica</i>)												
Sauk: in bloom (b)	5/23-6/14	5/23-6/21	6/3-7	6/13-7	6/5-6/28	6/1
Dane: in bloom	6/6-7/15	6/17-7/16	(6/12)
158 BAPTISIA (<i>Baptisia leucophaea</i>)												
Sauk: in bloom	6/14-7/10	6/4-7	5/15-5/29	6/1-7	6/1
159 SPIDERWORT (<i>Tradescantia reflexa</i>)*												
Sauk: in bloom	6/7-7	6/4-7/3	5/27-6/30	6/9-7	5/23-6/30	5/30-7/19	6/4-7/19	5/29-7/15	6/13-7/20	6/2
Dane: in bloom	6/8-7	5/25-7	6/5-7/23	6/1-7/29	6/2

Species, Station, Item	1935	1936	1937	1938	1939	1940	1941	1942	1943	1944	1945	Average
160 ANGELICA (<i>Angelica atropurpurea</i>)												
Dane: in bloom.....							5/31-?	6/2-?	6/9-?	6/3-6/22	5/28-6/27	6/2
161 ALSIKE CLOVER (<i>Trifolium hybridum</i>)												
Sauk: first bloom.....				6/8				5/24	6/5	6/2	6/5	6/3
162 PENSTEMON (<i>Penstemon gracilis</i>)												
Sauk: in bloom (b).....						6/8-?	5/23-?	5/30-?	6/5-?	5/28-?	6/16-7/5	6/3
163 CANADA MAYFLOWER (<i>Maianthemum canadense</i> var. <i>interius</i>)												
Sauk: first bloom.....						6/1			6/3	5/28	6/12	6/3
164 DEWBERRY (<i>Rubus flagellaris</i>)*												
Sauk: in bloom.....						6/8-?	5/29-6/11	5/30-6/22	6/5-6/26	6/3-6/27	6/5-7/3	6/3
fruit ripe.....				7/17-8/13		7-8-30		7/21-?	7/25-?	7/27-?	7/28-9/3	7/21
165 DOMESTIC YELLOW IRIS (<i>Iris flavescens</i>)												
Sauk: in bloom.....									6/4-?	6/1-?	6/5-6/20	(6/3)
166 ANEMONE (<i>Anemone canadensis</i>)												
Sauk: in bloom.....			6/13-?	6/4-?	5/27-6/24	6/13-?	5/23-7/1	5/30-7/21	6/3-7/21	5/29-7/15	6/5-7/25	6/3
Dane: in bloom.....				5/28-?				5/30-?				(5/29)
167 FROSTWEED (<i>Helianthemum canadense</i>)												
Dane: in bloom.....							5/27-?			6/7-6/27	6/7-7/22	(6/3)
168 WHITE CLOVER (<i>Trifolium repens</i>)												
Sauk: first bloom.....							6/7	6/1	6/2	6/2	6/5	6/3
Dane: first bloom.....				5/31	5/29	6/3	5/27	5/30		6/1	5/29	5/30
169 YARROW (<i>Achillea Millefolium</i>)												
Sauk: in bloom.....					6/11-?	6/9-?	5/30-6/30	5/30-7/19	6/2-7/21	6/1-7/15	6/5-9/3	6/4
Dane: in bloom.....				5/28-?				5/30-?		6/2-8/20	6/3-8/1	5/31
170 WOODCOCK (<i>Philohela minor</i>) Last peenting.												
Sauk:.....			6/7		6/1	6/2+	5/31	6/1	6/3+	5/31	6/16	6/4
Dane:.....				5/24+	6/5					5/28		(6/1)
171 NINEBARK (<i>Physocarpus opulifolius</i>)												
Sauk: in bloom.....					6/4-6/11	6/13-?	5/29-6/7	6/1-6/13	6/10-6/21	6/1-6/9	6/5-6/20	6/4
Dane: in bloom.....										6/5-6/15	6/8-6/28	(6/7)
Leafing is completed before blooming.												
172 HUDSONIA (<i>Hudsonia tomentosa</i>)												
Sauk: in bloom (b).....									6/5-?	6/2-?	6/4-6/17	(6/4)
173 WILD PARSNIP (<i>Pastinaca sativa</i>)												
Dane: in bloom.....							6/7-?	5/31-?		6/5-7/30	6/6-7/29	6/4
174 SPATTERDOCK (<i>Nuphar variegata</i>)												
Sauk: in bloom.....					(by 5/19)			6/5-8/13	6/10-9/7	5/29-8/5	6/5-8/15	6/5
Dane: in bloom.....				5/31-?	5/27-?		5/24-?					(5/27)
175 BLACK LOCUST (<i>Robinia Pseudo-Acacia</i>)												
Sauk: in bloom.....					7-6/3		5/23-?	5/30-6/7	6/9-6/13	5/29-6/3	6/16-?	6/5
Dane: in bloom.....				5/29-?			5/23-?			5/28-6/4	6/6-6/14	5/29
Leafing is completed by the blooming period. Clones (thickets) differ from each other in leafing and blooming dates, but the trees within a clone, leaf and bloom together.												
176 KRIGIA (<i>Krigia biflora</i>)												
Sauk: in bloom.....							5/31-6/27	5/31-7/2	6/15-?	5/30-7/3	6/12-7/12	6/7
Dane: in bloom.....				6/10-?			5/27-?	5/9-?		6/11-6/30	6/15-7/13	6/2
177 LYCHNIS (<i>Lychnis alba</i>)												
Sauk: in bloom.....					6/17-?	(by 5/30)	5/29-?	5/23-7/26	6/11-8/2	6/13-7/17	6/12-9/15+	6/7
Dane: in bloom.....									6/9-?	5/29-8/21	5/30-?	(6/2)
178 RED CLOVER (<i>Trifolium pratense</i>)												
Sauk: first bloom.....									6/5	6/2	6/15	(6/7)
Dane: first bloom.....				6/7	6/7			5/29		6/5	6/5	6/4
179 POTENTILLA (<i>Potentilla arguta</i>)												
Sauk: in bloom.....								6/1-?	6/13-7/4	6/1-7/17	6/12-7/1	6/7
180 ASPARAGUS (<i>Asparagus officinalis</i>)												
Sauk: sprouts gathered								5/1-5/27	5/10-5/31	5/15-?	4/21-6/5	5/4
first bloom.....					(by 5/27)				6/5	6/1	6/16	(6/7)
181 YELLOW SWEET CLOVER (<i>Melilotus officinalis</i>)												
Sauk: first bloom.....							6/7	6/7	6/15	(by 6/13)	6/4	6/8
Dane: in bloom.....					(by 6/12)			5/31-?		5/31-7/8	5/31-7/25	(5/31)
182 DAISY (<i>Chrysanthemum leucanthemum</i> var. <i>pinnatifidum</i>)												
Sauk: in bloom.....									6/15-?	6/1-8/10	6/9-?	(6/8)
Dane: in bloom.....										6/2-8/15	6/1-8-24	(6/2)

Species, Station, Item	1935	1936	1937	1938	1939	1940	1941	1942	1943	1944	1945	Average
183 AMERICAN BITTERSWEET (<i>Celastrus scandens</i>)												
Sauk: in bloom.....	5/30-?	6/6-?	5/31-?	6/25-7/4	6/8
Dane: in bloom.....	5/30-?	6/1-?	(5/31)
184 MARSH BLUEFLAG (<i>Iris virginica</i> var. <i>Shrevei</i>)												
Sauk: in bloom.....	6/19-?	6/8-?	6/7-?	6/5-?	6/14-?	6/1-?	6/12-7/4	6/9
Dane: in bloom.....	6/4-6/26	6/1-?	6/2-?	6/5-6/28	6/10-6/28	6/4
185 MOCK ORANGE (<i>Philadelphus coronarius</i>)												
Dane: in bloom (b).....	6/13-6/27	6/2-6/22	6/12-7/4	(6/9)
186 SCRIBNER'S PANIC (<i>Panicum scribnerianum</i>)												
Sauk and Dane:
in head.....	5/22	5/22	5/29	5/28	6/5	5/27
in pollen.....	6/2-?	6/17-7/3	(6/9)
seed ripe.....	6/25-?	7/5-?	7-7/26	7/5-7/25	7/5-?	7/8-?	7/3
187 FIREFLY (Family <i>Lampyridae</i>) First seen.												
Sauk:.....	6/13	6/11	5/31	6/7	6/14	6/15	6/12	6/11
Dane:.....	6/10	6/14	6/15	(6/13)
188 DAISY FLEABANE (<i>Erigeron ramosus</i>)												
Sauk: in bloom.....	6/13-?	6/7-?	6/7-8/13	6/14-?	6/13-8/7	6/16-9/10	6/12
Dane: in bloom.....	5/28-?	5/28-8/21	6/13-8/10?	(6/2)
189 NORTHERN BEDSTRAW (<i>Galium boreale</i>)												
Sauk: in bloom.....	6/19-7/11	6/15-7/5	6/11-7/5	7-7/25	(6/12)
Dane: in bloom.....	6/7-?	6/9-?	6/7-7/16	6/15-7/23	(6/10)
190 POISON IVY (<i>Rhus radicans</i>)												
Sauk: in bloom.....	5/30-6/22	6/17-6/25	6/5-?	6/27-?	6/12
191 BLUETS (<i>Houstonia caerulea</i>)												
Sauk: in bloom.....	7-6/30	6/23-7/5	6/1-7/9	6/21-6/31	6/1-7/15	6/12
192 HAREBELL (<i>Campanula rotundifolia</i>)												
Sauk: in bloom.....	(by 6/11)	6/13-?	6/7-8/24	6/7-8/9	6/15-8/31	6/15-7/17	6/16-9/16+	6/12
193 LOBELIA (<i>Lobelia spicata</i>)												
Sauk: in bloom.....	7-7/12	7-7-10	6/25-7/14	(6/25)
Dane: in bloom.....	6/7-?	6/13-7/26	6/16-7/28	(6/12)
194 WHITE WILD INDIGO (<i>Baptisia leucantha</i>)												
Sauk: in bloom.....	7/1-?	6/15-?	6/4-?	6/13-?	6/3-6/30	6/7-7/26	6/15-7/9	6/11-7/5	6/17-7/29	6/13
Dane: in bloom.....	6/3-?	6/4-7/2	6/14-7/25	(6/7)
195 GREY DOGWOOD (<i>Cornus racemosa</i>)												
Sauk: in bloom.....	6/4-6/18	6/20-?	6/1-?	6/7-6/22	6/17-?	6/15-?	6/25-?	6/13
Dane: in bloom.....	6/9-?	6/4-6/19	6/15-7/5	(6/9)
196 FLOWERING SPURGE (<i>Euphorbia corollata</i>)												
Sauk: in bloom.....	6/25-8/20	6/17-?	6/16-?	6/29-9/7	6/1-9/7	6/1-9/7	6/2-8/31	6/16-9/10	6/13
Dane: in bloom.....	6/9-?	6/24-8/21	6/17-?	(6/13)
This plant bears a few preliminary blossoms a month before full bloom begins. Failure to detect these may account for the large spread of dates as between years.												
197 QUACK GRASS (<i>Agropyron repens</i>)												
Sauk: in head.....	6/3	6/13	6/10	6/25	6/12
first pollen.....	6/8-?	5/31	6/15	6/25	6/19	7/5	6/13
Dane: in head.....	6/3	6/3	6/8	6/1	6/3	6/4
in pollen.....	6/17-?	6/26-7/25	(6/21)
198 GROUND CHERRY (<i>Physalis virginiana</i>)												
Dane: in bloom.....	6/9-?	6/12-7/9	6/17-7/11	(6/13)
199 WILD CARROT (<i>Daucus carota</i>)												
Dane: in bloom.....	6/29-?	5/26-8/25	6/9-?	6/23-8/31	6/9-9/5	6/13
200 ALFALFA (<i>Medicago sativa</i>)												
Jefferson: first bloom.....	6/9	6/11	6/14	6/16	6/9	6/22	6/17	6/28	6/14
Jefferson: first mowing.....	6/20-7/20	6/17-7/8	6/15-7/7	6/10-7/10	6/17-7/25	6/22-7/18
Data from McCabe and Hawkins (Fig. 6).												
201 SILKY DOGWOOD (<i>Cornus obliqua</i>)												
Sauk: in bloom.....	7-6/24	6/8-?	6/7-?	6/7-6/23	6/19-7/5	6/15-7/5	6/25-7/20	6/14
202 SOLOMON'S SEAL (<i>Polygonatum biflorum</i>)												
Sauk: in bloom.....	6/15-6/25	6/15-7/4	6/9-?	6/17-7/4	6/14
Dane: in bloom.....	5/26-6/21	6/12-6/28	(6/3)
203 WAHOO (<i>Eriogonum atrorubescens</i>)												
Sauk: in bloom (b).....	6/12-7/5	6/7-?	6/7-6/30	6/7-7/12	6/25-7/10	6/13-7/5	7/1-?	6/14

The fruits turn pink in September, are red and open through October, and lose color about November 10.

Species, Station, Item	1935	1936	1937	1938	1939	1940	1941	1942	1943	1944	1945	Average
204 TALL MEADOW RUE (<i>Thalictrum dasycarpum</i>)												
Sauk: in bloom.....					6/17-?		6/14-?	6/10-7/15	6/17-7/10	6/13-7/15	6/20-7/20	6/15
Dane: in bloom.....										6/4-7/1	6/17-7/17	(6/10)
205 HEDGE BINDWEED (<i>Convolvulus sepium</i>)												
Sauk: in bloom.....							6/7-?	6/15-8/15	6/26-8/20	6/15-?	6/12-8/20	6/15
Dane: in bloom.....				6/23-?						6/5-?	6/23-9/23	6/17
206 FIELD BINDWEED (<i>Convolvulus arvensis</i>)												
Dane: first bloom.....									6/19	6/7	6/22	(6/15)
207 WHITE SWEET CLOVER (<i>Melilotus alba</i>)												
Sauk: in bloom.....					6/19-?			7-7/31	7-7/26	7-8/5	6/16-9/1	(6/17)
Dane: in bloom.....				5/31-?						6/15-8/2	6/13-9/5+	(6/9)
208 MOTHERWORT (<i>Leonurus Cardiaea</i>)												
Dane: in bloom.....				6/14-?						6/21-8/1	6/16-8/15	(6/17)
209 CATALPA (<i>Catalpa speciosa</i>)												
Dane: in bloom.....				(by 7/12)	6/19-?	6/17-?			7-6/28	6/8-6/23	6/27-7/13	6/18
This is the collective record of 10 trees in Madison. In 1945 some individual trees in nearby villages bloomed 2 weeks later.												
210 NORTHERN VIRGINIA DEER (<i>Odocoileus virginianus borealis</i>) First record of full red pelage.												
Sauk:.....			6/26			7/12			5/29	6/13	6/10	6/18
211 MILKWEED (<i>Asclepias amplexicaulis</i>)												
Sauk: in bloom.....										6/11-6/25	7/1-7/20	(6/21)
Dane: in bloom.....										6/14-7/4	6/25-7/15	(6/20)
212 ELDERBERRY (<i>Sambucus canadensis</i>)												
Sauk: in bloom.....					6/17-7/9	(by 7/1)	6/10-7/1	6/22-7/12+	6/17-7/20+	6/17-7/10+	7/1-8/10	6/21
Dane: in bloom.....				6/20-?					6/23-7/14	6/17-?	6/26-8/14	6/21
Sauk & Dane: fruit ripe				(by 9/5)			8/8-?	8/13-9/11	8/15-9/20	7-9/15	9/7-?	8/18
213 BLACK EYED SUSAN (<i>Rudbeckia hirta</i>)												
Sauk: in bloom.....				6/25-?	6/17-?	7/6-?	6/14-?	6/22-7/31	6/21-8/1+	6/15-7/28+	6/28-9/3	6/22
Dane: in bloom.....				6/23-?			6/5-?	(by 6/19)		6/15-8/1	6/25-8/27	6/17
214 VENUS LOOKING-GLASS (<i>Specularia perfoliata</i>)												
Sauk: in bloom.....							6/14-?			6/15-?	6/28-7/20	(6/22)
215 CANADA THISTLE (<i>Cirsium arvense</i>)												
Dane: in bloom.....							6/15-?		6/30-7/20	6/21-8/20	6/28-8/12+	6/23
216 SMOOTH SUMAC (<i>Rhus glabra</i>)												
Sauk: in bloom.....							6/19-?	6/22-?	6/25-7/5	6/17-6/29	7/8-?	6/24
Dane: in bloom.....										6/23-7/1	7/5-7/22	(6/29)
Leafing and growing precede bloom.												
217 WHITE WATER LILY (<i>Nymphaea tuberosa</i>)												
Sauk: in bloom.....				6/25-?		(by 7/12)	7/1-?	6/22-?	6/26-9/7	6/13-?	6/25-9/10	6/24
218 CHICORY (<i>Cichorium intybus</i>)												
Dane: first bloom.....							6/24		6/24	6/19	6/29	6/24
Full bloom.....				(by 7/10)					7/15	6/29	7/10	(7/8)
219 SPREADING DOGBANE (<i>Apocynum androsaemifolium</i>)												
Sauk: in bloom (b)...							6/14-?	6/22-?	6/26-?	6/25-?	7/8-?	6/25
Dane: in bloom.....				6/21-?						6/23-?	7/3-8/14	(6/26)
220 DOG FENNEL (<i>Anthemis cotula</i>)												
Sauk: in bloom.....				6/23-?				6/21-7/29		6/28-9/4	6/28-8/15	6/25
221 ORANGE DAY LILY (<i>Heimerocallis fulva</i>)												
Sauk: in bloom (b)...							6/16-?	6/27-7/28	6/29-7/25	6/27-7/28	7/2-8/1	6/26
Dane: in bloom.....									6/29-?	6/27-?	6/29-?	(6/28)
222 ST. JOHN'S WORT (<i>Hypericum perforatum</i>)												
Sauk: in bloom.....							6/19-?	6/23-7/25+	6/26-7/19+	6/29-7/17+	7/1-8/5	6/26
Dane: in bloom.....										6/29-7/24	7/2-8/12	(7/1)
223 PURPLE LOOSESTRIFE (<i>Lythrum alatum</i>)												
Dane: in bloom.....									6/23-7/27	6/23-7/30	7/6-8/25	(6/27)
224 COWBANE (<i>Cicuta maculata</i>)												
Sauk: in bloom.....							7-8/2	6/26-8/20	6/27-8/17	7/1-8/8		(6/28)
Dane: in bloom.....							6/3-?		6/25-8/14	6/25-8/17		(6/17)
225 BUTTER AND EGGS (<i>Linaria vulgaris</i>)												
Sauk: in bloom.....						7/6-?		6/23-9/15+	7/5-8/20+	7/1-8/20+	6/16-9/15+	6/28
Dane: in bloom.....				7/10-?			6/7-?			6/15-8/28+	6/27-?	(6/22)

In 1944, in Sauk, bloom ceased during an August drouth, but resumed Sept. 1-Oct. 17.

Species, Station, Item	1935	1936	1937	1938	1939	1940	1941	1942	1943	1944	1945	Average
226 TIMOTHY (<i>Phleum pratense</i>)												
Sauk: in head.....	6/13	6/15	6/15	6/16	6/15
in pollen.....	(by 6/23)	7/1-?	6/23-?	6/22-7/21	6/23-7/9+	6/27-7/10+	7/1-7/25	6/28
Dane: in pollen.....	6/23-?	6/18-7/10	6/28-7/25	(6/23)
227 BLACK BINDWEED (<i>Polygonum convolvulus</i>)												
Sauk: in bloom.....	6/27-?	7/1-?	7/3-?	(6/30)
228 NEW JERSEY TEA (<i>Ceanothus americanus</i>)												
Sauk: in bloom (b).....	(by 6/27)	6/27-7/23	6/27-7/24	6/29-7/17+	7/9-8/8	6/30
Dane: in bloom.....	7/10-?	6/27-?	6/21-?	7/11-?	7/2	7/2

TABLE 7. Phenology for July.

229 RED RASPBERRY (<i>Rubus idaeus</i> var. <i>strigosus</i>)												
Sauk: fruit first ripe.....	6/29	6/22	7/1	7/11	7/1
Dane: in fruit.....	6/30-?	7/10-8/15	7/1-7/15	6/28-7/22	7/2

This species blooms about June 1. The flowers are heavily used by bees.

230 COREOPSIS (<i>Coreopsis palmata</i>)												
Sauk: in bloom.....	6/19-?	7/1-8/5	7/5-?	7/1-7/17	7/11-8/9	7/1
Dane: in bloom.....	(by 7/10)	7/1-7/22	7/7-8/15	(7/4)
231 FRINGED LOOSESTRIFE (<i>Lythrum latifolium</i>)												
Sauk: in bloom.....	6/19-?	7-8, 15	7/9-8/23	6/29-8/7	7/8-8/20	7/1
Dane: in bloom.....	6/25-8/20+	7/2-8/24	(6/28)
232 COMMON MILKWEED (<i>Asclepias syriaca</i>)												
Sauk: in bloom.....	7/9-?	7/8-?	7/1-8/2	6/26-7/20	6/29-7/19	7/3-8/5	7/2
Dane: in bloom.....	7/6-?	6/21-7/30	7/3-8/24	(7/1)
233 BASSWOOD (<i>Tilia americana</i>)												
Sauk: in bloom.....	7/1-?	7-7/12	7/5-?	(7/3)
Dane: in bloom.....	6/29-7/8	6/27-7/10	7/7-7/19	(7/1)

At the Sauk station basswood is often so severely defoliated by cankerworm that no bloom occurs.

234 RAGGED ORCHIS (<i>Habenaria lacera</i>)												
Sauk: in bloom.....	7/1-7/21	7/1-?	6/29-7/15	7/10-8/1	7/3
235 HOLLYHOCK (<i>Althaea rosea</i>)												
Sauk: in bloom (b).....	7/6-?	7/1-8/13	7/5-?	7/1-8/7	7/3-8/15	7/4
Dane: in bloom.....	7/3-?	6/25-?	6/28-8/27	(6/29)
236 VERONICASTRUM (<i>Veronicastrum virginicum</i>)												
Sauk: in bloom.....	7-7/21	7/1-?	7/12-8/2	6/29-?	7/1-8/15	7-8/22	7/4-8/7	7/8-8/12	7/4
Dane: in bloom.....	7/5-?	7/2-8/13	7/6-8/23	(7/4)
237 BLUE VERVAIN (<i>Verbena hastata</i>)												
Sauk: in bloom.....	6/29-?	7/5-8/31	7/5-9/7	7/4-9/9	7/8-9/5	7/4
Dane: in bloom.....	7/16-?	7/4-?	6/18-?	7/3-?	7/15-?	6/26-8/21	7/6-9/2+	7/4
238 MILKWORT (<i>Polygala sanguinea</i>)												
Sauk: in bloom.....	7/1-?	7/6-?	7/3-8/23+	7/5-8/31+	7/1-8/31+	7/8-9/15+	7/4
Dane: in bloom.....	7/1-8/20+	7/14-?	(7/7)

A few blooms every year straggle through September.

239 MULLEIN (<i>Verbascum Thapsus</i>)												
Sauk: in bloom.....	7/6-?	7/12-8/13	7/5-?	7-9/5	6/28-8/15+	7/5
Dane: in bloom.....	6/23-?	7/1-?	6/30-?	7/5-?	7/2-9/17	6/28-8/30+	6/29
240 GERMANDER (<i>Teucrium canadense</i>)												
Sauk: in bloom.....	7/4-7/26	7/6-7/25	7/1-?	7/8-8/25	7/5
Dane: in bloom.....	7/14-8/20+	7/2-8/18	(7/8)
241 BUTTERFLY WEED (<i>Asclepias tuberosa</i>)												
Sauk: in bloom.....	7/2-?	7/15-?	6/29-?	7/1-8/3	7/5-8/21	7/1-8/7	7/13-8/31	7/5
Dane: in bloom.....	7/11-?	7/9-8/8	(7/10)

This plant, like many other prairie forbs, does not emerge until late. The first sprouts appear about June 1 and are a foot high by mid-June.

242 EVENING PRIMROSE (<i>Oenothera pycnocarpa</i>)*												
Sauk: in bloom.....	(by 7/6-?)	7/5-8/23+	7/5-8/21+	7/1-8/20+	7/9-8/25+	7/5
Dane: in bloom.....	7/12-8/20+	7/11-8/29	(7/11)
243 POINTED LEAF TICK CLOVER (<i>Desmodium acuminatum</i>)												
Dane: in bloom.....	7/4-?	6/29-8/13	7/13-8/25+	(7/5)
244 MARSH MILKWEED (<i>Asclepias incarnata</i>)												
Sauk: in bloom.....	7/7-?	7/12-?	6/27-?	7-8/15	7-8/21	7/3-8/7	7/11-8/20	7/6
Dane: in bloom.....	7/8-?	6/28-8/15	7/13-8/24	(7/6)

Robert A. McCabe (unpubl.) points out that the fibrous bark of this plant constitutes the principal nesting material for alder flycatcher and gold finch on the University Arboretum. Only the dead stems of the previous year yield fibre, older ones being completely stripped.

Species, Station, Item	1935	1936	1937	1938	1939	1940	1941	1942	1943	1944	1945	Average
245 HORSEMINT (<i>Monarda punctata</i> var. <i>villicaulis</i>)												
Sauk: in bloom.....	(by 7/20)	7/1-8/25	7/5-8/22	7/1-8/7+	7/20-9/1+	7/7
246 LEAD PLANT (<i>Amorpha canescens</i>)												
Sauk: in bloom.....	7/5-7/31	7/7-7/25	7/1-7/19	7/20-8/10	7/8
Dane: in bloom.....	7/12-?	6/26-7/21	7/4-8/17†	(7/4)
247 MEADOWSWEET (<i>Spiraea alba</i>)												
Sauk: in bloom.....	7/20/8-2	6/29-?	7/5-7/31+	7/9-?	7/15-?	7/3-8/15+	7/8
248 TURKSCAP LILY (<i>Lilium michiganense</i>)												
Sauk: in bloom.....	7-7/29	7-7/28	7/5-7/23	7/10-?	7/1-7/28	7-8/1	7/5-7/20	7/25-8/10	7/9
Dane: in bloom.....	7/8-?	6/28-8/3	7/23-8/14	(7/9)
249 LOPSEED (<i>Phryma leptostachya</i>)												
Dane: in bloom.....	7/15-?	7/1-8/6	7/11-8/12	(7/9)
250 SMARTWEED (<i>Polygonum pennsylvanicum</i>)												
Sauk: in bloom.....	7/12-?	7/1-8/31	7-9/6	7/5-9/1	7/20-9/15	7/10
251 GREEN MILKWEED (<i>Asclepias viridiflora</i>)												
Sauk: in bloom.....	7/1-?	7-8/13	7/5-7/25	7/25-?	(7/10)
252 HORSE NETTLE (<i>Solanum carolinense</i>)												
Sauk: in bloom.....	7/11-?	7/9-?	7-8/8	7/10
253 PRAIRIE WHITE FRINGE ORCHID (<i>Habenaria leucophaea</i>)												
Dane: in bloom (b).....	7/9-?	7/4-?	7/12-7/31	7/16-8/8	7/10
254 CATNIP (<i>Nepeta Cataria</i>)												
Sauk: in bloom.....	7/8-?	7/15-8/23	7/5-?	7/5-8/7+	7/20-8/28	7/11
Dane: in bloom.....	7/7-?	7/5-?	7/1-8/20+	7/13-?	7/7
255 COMMON PLANTAIN (<i>Plantago Rugelii</i>)												
Sauk: first bloom.....	7/19	(by 7/9)	7/3	7/11
256 WINTER RYE (<i>Secale cereale</i>)												
Dane: ripe and cut.....	7/8	7/5	7/16	7/7	7/12	7/13	7/22	7/11
257 PRAIRIE DOCK (<i>Silphium terebinthinaceum</i>)												
Prairie du Sac:
in bloom.....	7/27-8/29	7/12-8/31	(7/19)
Dane: in bloom.....	7/13-?	7/13-?	7/3-?	7/12-9/6	7/12-9/18	7/11
258 BOUNCING BET (<i>Saponaria officinalis</i>)												
Sauk: in bloom.....	7/19-8/23	7/7-8/21+	7/1-8/3	7/20-9/15	7/12
Dane: in bloom.....	(by 7/14)	(by 7/10)	7/8-?	6/23-?	6/30-9/28†	(6/30)
This weed nearly always straggles. In 1944 in Sauk County it ceased bloom during an August drouth, but then straggled through September.												
259 WILD BERGAMOT (<i>Monarda fistulosa</i>)												
Sauk: in bloom.....	7/1-?	(by 7/15)	7/10-8/15	(by 7/13)	7-8/9	7/25-8/12+	7/12
Dane: in bloom.....	7/8-?	7/6-?	7/3-?	7-8/7	7/3-7/16	7/14-8/29+	7/7
260 WHITE PRAIRIE CLOVER (<i>Petalostemum candidum</i>)												
Sauk: in bloom.....	7/1-?	7-8/15	7/9-?	7/10-?	7/27-8/24	7/12
Dane: in bloom.....	7/2-7/25	7/18-?	(7/11)
261 PURPLE PRAIRIE CLOVER (<i>Petalostemum purpureum</i>)												
Sauk: in bloom.....	7/1-?	7/10-8/2	7-8/21	7/10-8/3	7/27-8/27	7/12
Dane: in bloom.....	7-8/1	7/9-?	7/26-?	(7/17)
262 HAIRY HAWKWEED (<i>Hieracium longipilum</i>)												
Sauk: in bloom.....	7/1-8/15	7/24-8/15	7/4-8/15	7/25-8/20	7/14
Dane: in bloom.....	7/5-8/13	7/17-9/7	(7/11)
63 WHITE VERVAIN (<i>Verbena urticifolia</i>)												
Sauk: in bloom.....	7-8/7	7/23-?
Dane: in bloom.....	7/25-?	7/8-?	7/11-9/3	(7/14)
264 CUTLEAF CONEFLOWER (<i>Ratibida pinnata</i>)												
Sauk: in bloom.....	7/20-?	7/9-8/29	7/5-8/7	7/25-9/15	7/15
Dane: in bloom.....	7-8/29	7/5-8/25	7/13-?	7/9
265 NORTHERN VIRGINIA DEER (<i>Odocoileus virginianus borealis</i>) First record of fawns travelling with doe.												
Sauk:.....	7/18	7/22	7/6	(7/15)
266 CANADA NETTLE (<i>Laportea canadensis</i>)												
Sauk: in bloom.....	(by 7/29)	7/17-8/15+	7/5-?	7-8/7	7/25-?	(7/16)
267 CICADA (Probably <i>Tibicen linnei</i>) No specimen identified. First heard.												
Sauk:.....	7/19	7/19	7/3	7/25	7/17
Dane:.....	7/19	6/15	7/21	(7/8)
268 PICKEREL WEED (<i>Pontederia cordata</i>)												
Sauk: in bloom.....	(by 7/28)	7/22-?	7/19/8/13	7/25-9/7	7/1-9/9	7/25-8/20	7/18
Dane: in bloom.....	6/23-8/20+	7/13-9/9	(7/3)

Species, Station, Item	1935	1936	1937	1938	1939	1940	1941	1942	1943	1944	1945	Average
269 BUTTON BUSH (<i>Cephalanthus occidentalis</i>)												
Sauk: in bloom (b)...	7/23-8/3	7/13-8/2	7-8/1	7/9-7/19	7/29-7	7/18
Dane: in bloom.....	7/15-8/1+	7/9-7/25+	7/20-8/25+	(7/15)
270 RATTLESNAKE MASTER (<i>Eryngium yuccaefolium</i>)												
Sauk: in bloom (one plant, introduced) (b)...	7-8/2	7/15-8/5	7/20-8/28	(7/18)
Dane: in bloom.....	7-8/11	7/26-7	7/10-8/10	7-19-9/4	(7/18)
271 RUDBECKIA (<i>Rudbeckia laciniata</i>)												
Sauk: in bloom (b)...	7-8/28	7/15-7	7/20-7	7/12-8/23	7/23-9/10	7/17-9/9	7/25-9/16	7/19
272 OATS (<i>Avena sativa</i> var. <i>Vickland</i>) (See 62 for sowing dates).												
Dane: first ripe.....	7/23	7/19	7/14	7/20	7/20	7/23	7/17	7/23	7/25	7/20
Data from University Farms by courtesy of Prof. H. L. Shands, Dept. of Agronomy, College of Agriculture. Cutting is usually about 2 days after ripening.												
273 IRONWEED (<i>Vernonia fasciculata</i>)												
Sauk: in bloom.....	7/23-7	7/11-8/10	7/22-7	7/12-8/20+	7/23-8/31	7/17-8/31+	8/10-9/15	7/21
Dane: in bloom.....	7/20-7	7/18-8/20+	8/7-9/20	(7/25)
274 COMPASSPLANT (<i>Silphium laciniatum</i>)												
Prairie du Sac:												
in bloom (b)...	7/9-7	7/10-7	7/27-8/27	(7/23)
Dane: in bloom.....	7/20-8/25	7/10-7	7/17-9/16	(7/16)
275 JOE-PYE-WEED (<i>Eupatorium maculatum</i>)												
Sauk: in bloom.....	7/15-7	7/27-9/19	7/24-9/7+	7/18-9/1	7/29-9/16	7/23
Dane: in bloom.....	7/30-7	7/11-7	7-9/1	7/17-9/1	7/23-9/21	7/20
276 LIATRIS (<i>Liatris pycnostachya</i>)												
Sauk: in bloom.....	7/23-7	7/23-7	7/15-7	7/27-7	7-8/24	7/21-8/23	7/25-8/23	7/20-7	8/3-8/30	7/24
Dane: in bloom.....	7/25-7	7/20-7	7/23-7	7/25-7	7/11-7	7/17-9/2	7/20
This species has visible buds for nearly a month before it blooms.												
277 EARLY GOLDENROD (<i>Solidago juncea</i>)												
Sauk: first bloom.....	(by 7/30)	7/23-7	7/29-7	7/20-7	7/19-7	7/25-7	7/27-7	7/25-7	7/24
Dane: first bloom.....	7/25-7	7/20-7	7/22-7	7/18-8/20+	7/19/8-22	7/21
278 SUNFLOWER (<i>Helianthus occidentalis</i>)												
Sauk: in bloom (b)...	7-8/31	7/29-9/7	7/21-9/10	7/25-9/9	(7/25)
279 CANADA TICK CLOVER (<i>Desmodium canadense</i>)												
Sauk: in bloom.....	(by 7/28)	7/27-7	7/19-7	8/1-8/21	7/17-8/7	8/5-8/26	7/26
Dane: in bloom.....	7/12-8/17	7/19-9/4	(7/11)
280 MALLARD (<i>Anas platyrhynchos platyrhynchos</i>) Young seen flying.												
Sauk:	7/21	8/5	7/20	7/19	7/25	8/3	7/27	7/26
281 BONESET (<i>Eupatorium perfoliatum</i>)												
Sauk: in bloom.....	7/22-7	7/23-9/11	7-9/7	7/28-9/5	8/5-9/15	7/27
Dane: in bloom.....	7/3-7	7/20-7	7/23-9/17	7/23-10/1	7/17
282 BULL THISTLE (<i>Cirsium vulgare</i>)												
Sauk: in bloom.....	7-8/23+	7/25-8/27+	7/27-7	7/28-9/15+	(7/27)
Dane: in bloom.....	7/25-7	7/12-7	7/14-7	7/25-9/22	7/27-7	7/21
283 TANSY (<i>Tanacetum vulgare</i>)												
Prairie du Sac:												
in bloom (b)...	8/2-7	7/21-8/29	7/25-7	7/29-9/15	7/27
Dane: in bloom.....	8/1-7	7/24-9/23	8/5-7	(7/31)
284 PRAIRIE CORDGRASS (<i>Spartina pectinata</i>)												
Sauk: in pollen.....	7/29-7	7-8/17	7/21-8/15	7-8/21	8/1-7	7/28-7	7/27
285 ARROWHEAD (<i>Sagittaria latifolia f. gracilis</i>)												
Sauk: first bloom.....	(by 7/27)	8/1	7/7	(by 7/13)	8/10	(7/27)
286 PRICKLY LETTUCE (<i>Lactuca scariola</i>)												
Sauk: in bloom.....	7/14-7	8/5-7	7/30-8/21	7-8/21	7-8/25	(7/27)
287 CARDINAL FLOWER (<i>Lobelia cardinalis</i>)												
Sauk: in bloom.....	8/1-7	7/30-7	8/1-7	7-8/24	8/2-9/13	7-9/17	7/19-9/21	7/29-9/15	7/29
288 SQUIRRELS (Fox and Gray) First eat burr oak acorns.												
Sauk and Dane:.....	8/11	8/5	7/22	7/21	7/30
289 CANADA FLEABANE (<i>Erigeron canadensis</i>)												
Sauk: first bloom.....	8/2	(by 7/12)	7/29	8/1	8/1	7/29	7/31
Dane: in bloom.....	7/18-7	7/24-8/20+	7/31-7	(7/24)
290 BIG BLUESTEM (<i>Andropogon furcatus</i>)												
Sauk: in pollen.....	7/27-7	7/26-8/13	7/26-8/21	8/4-7	8/9-9/8	7/31
Dane: in pollen.....	7-8/29	7/21-8/26	8/2-9/16	(7/27)

Species, Station, Item	1935	1936	1937	1938	1939	1940	1941	1942	1943	1944	1945	Average
291 WHITE PINE (<i>Pinus Strobus</i>) Bud scales first shed from new growth.												
Sauk:.....					7/25			7/30	8/2	8/1	8/5	7/31

TABLE 8. Phenology for August.

292 BURDOCK (<i>Ardiuminus</i>)												
Sauk: first bloom.....								8/2	7/27	8/1	8/10	8/1
Dane: in bloom.....								8/1-?	7/22-?	7/23-8/8	8/2-9/30	7/28
293 WHITE SNAKEROOT (<i>Eupatorium rugosum</i>)												
Sauk: in bloom.....							7-9/20	8/2-9/20		7-10/5	8/5-10/1	(8/4)
Dane: in bloom.....									8/23-9/23	7/9-9/1+	7/23-?	(7/29)
294 YELLOW FOXGLOVE (<i>Aureolaria</i> sp.)*												
Sauk: in bloom.....					8/4-8/25	8/5-8/20		8/2-8/23	7-9/1		7-9/8	(8/4)
295 GREAT RAGWEED (<i>Ambrosia trifida</i>)												
Dane: in bloom.....			8/17-9/1	8/1-?			8/8-?		8/7-?	7/30-9/3+	8/7-?	8/8
296 AMERICAN EGRET (<i>Casmerodias albus egretta</i>) Wandering young first seen.												
Sauk:.....				8/13	8/5	none	none	none	none	none	none	(8/9)
Dane and Jefferson: ..			7/5	7/28	8/15	9/12	8/6	8/?			8/8	8/2
297 SQUIRRELS (Fox, Gray, and Red) First eat hickory nuts.												
Sauk:.....			(by 8/28)		8/19		8/23	8/13	8/20	7/20	no nuts	8/13
298 LESSER RAGWEED (<i>Ambrosia artemisiifolia</i>)												
Sauk: in bloom.....					7/29-?	8/15-?	7-9/14	8/15-9/13	8/23-9/1	8/6-9/15	8/24-9/15	8/13
Dane: in bloom.....									8/9-?	7/30-8/20+	8/7-9/28	(8/5)
299 BUSH CLOVER (<i>Lespedeza capitata</i>)												
Sauk: in bloom.....						8/24-?		8/7-9/10	7-8/22	8/7-9/1	8/20-9/1	8/14
Dane: in bloom.....						(by 8/11)				7/30-8/21	8/8-9/6	(8/4)
300 LIATRIS (<i>Liatris spherioidea</i>)*												
Sauk: in bloom.....					8/19-9/10	8/20-?		8/7-9/7	7-9/13	7-9/17	8/10-9/15	8/14
Dane: in bloom.....			(by 8/1)	8/4-?						8/9-9/25	8/10-?	(8/6)
301 INDIAN GRASS (<i>Sorghastrum nutans</i>)												
Sauk: in bloom.....							8/31-?	8/29-?	8/11-8/25	8/17-8/29		8/15-8/26
Dane: in bloom.....									7-8/29	8/10-9/3	8/19-9/22	(8/15)
302 FUNKIA (<i>Funkia lanceolata</i>)												
Sauk: first bloom (b).....					8/25		8/24	(by 8/13)	8/21		8/15	8/21
303 NEW ENGLAND ASTER (<i>Aster novae-angliae</i>)												
Dane: first bloom.....			9/3	8/14				8/12	8/28	8/29	8/14	8/22
304 WHITE ASTER (<i>Aster pilosus</i>)*												
Sauk: in bloom.....							7-10/9		7-10/19	7-10/14	8/24-?	(8/24)
305 BLUE ASTER (<i>Aster laevis</i>)												
Sauk: first bloom.....							7-10/9	7-10/26		7-10/14	8/24-?	(8/24)
306 PRAIRIE GOLDENROD (<i>Solidago rigida</i>)												
Sauk: in bloom.....						9/3-9/25		8/23-9/15	8/21-9/31	9/1-9/20	8/25-9/20	8/25
Dane: in bloom.....								8/14-?		8/15-?	8/15-9/27	(8/15)
307 BIDENS (<i>Bidens cernua</i>)												
Sauk: in bloom.....							8/22-?		9/1-9/27	9/1-?	8/26-10/1	8/28

TABLES 9-12. Phenology for September to December.

308 CLOSED GENTIAN (<i>Gentiana Andrewsii</i>)												
Sauk: in bloom.....					9/3-?	9/6-10/12	8/23-?	9/1-?	9/1-10/15	9/1-10/12	8/30-10/5	9/1
309 SHAGBARK HICKORY (<i>Carya ovata</i>) Nuts ripe (hulls peel).												
Sauk:.....	9/5	9/2	9/25		9/3		9/7	9/1	9/5		no nuts	9/5
310 POISON IVY (<i>Rhus radicans</i>)												
Sauk: leaves first show fall color.....							9/12	9/7	9/17	9/5	9/20	9/12
311 OAKS (<i>Quercus</i>) Sauk and Dane. Ripe acorns first fall.												
Red Oak.....		9/20		9/1					9/10	9/15	9/17	9/13
White Oak.....		9/8									9/10	(9/9)
312 WHITE THROATED SPARROW (<i>Zonotrichia albicollis</i>) First migrants arrive.												
Dane:.....	9/28	9/23	9/19	10/8	9/26	9/21	9/17	9/20		9/3	9/8	9/20
313 WHITE PINE (<i>Pinus Strobus</i>) Old needles die and fall.												
Sauk:.....							(before 10/11)	10/3	10/3	9/20	9/25	9/21
314 RED PINE (<i>Pinus resinosa</i>) Old needles die and fall.												
Sauk:.....							(before 10/11)		9/25	9/20	9/25	(9/23)

Species, Station, Item	1935	1936	1937	1938	1939	1940	1941	1942	1943	1944	1945	Average
315 SATZ-COLORED JUNC (<i>Juncus hyemalis hyemalis</i>) First arrival in fall.												
Dane:.....	9/28	9/23	9/25	9/22	10/2	10/4	9/22	9/19	9/6	9/23
316 RUFFED GROUSE (<i>Bonasa umbellus</i>)												
Sauk: first fall drumming.....	9/27	9/20	9/30	(9/25)
317 RINGNECKED PHEASANT (<i>Phasianus torquatus</i>) First fall cackling and crowing.												
Sauk: crow.....	9/14	10/9	9/27	10/17	9/28	9/31
cackle.....	9/10	9/19	9/1	9/7	9/3	9/8	9/8
318 JACK PINE (<i>Pinus Banksiana</i>) Old needles turn yellow and fall.												
Sauk:.....	(by 10/29)	10/9	10/3	9/25	10/5	10/3
319 MUSKRAT (<i>Ondatra zibethica zibethica</i>) First house-building.												
Sauk and Dane:.....	10/1	10/25	9/27	10/1	9/25	10/4
320 CANADA GOOSE (<i>Branta canadensis canadensis</i>) First migrants arrive.												
Sauk:.....	10/14	10/21	10/11	9/23	10/16	10/14	10/5	10/11
Dane:.....	10/5	10/12	10/23	9/17	10/24	9/28	9/20	10/3	10/5
321 WAHOO (<i>Eonymus atropurpurea</i>) Fruits open.												
Sauk:.....	10/10	10/25	10/17	10/10	10/15	10/10	10/15
322 AMERICAN ROUGH-LEGGED HAWK (<i>Buteo lagopus s. johannis</i>) Arrives.												
Sauk and Dane:.....	11/11	10/27	10/10	10/27	10/18	10/25	9/9	11/4	10/14	10/16
323 FIRST KILLING FROST—Record by U. S. Weather Bureau.												
Dane:.....	10/4	10/23	10/13	11/7	10/14	11/11	10/28	9/25	10/17	10/15	9/29	10/17
Sauk:.....	9/29	10/1	10/8	10/25	10/14	10/15	9/29	9/25	10/17	10/11	9/29	10/7
324 NORTHERN VIRGINIA DEER (<i>Odocoileus virginianus borealis</i>) Bucks first rub horns.												
Sauk:.....	9/19	11/12	11/1	10/29	9/21	11/1	10/17
The variability in these dates arises from the fact that there are two periods for rubbing: in September, to clean the velvet, and in November, at the beginning of the rut.												
325 FALL CANKERWORM (<i>Anis opteryx pointaria</i>) Ascends trees.												
Sauk:.....	10/30-11/10	10/14-11/25	11/10-?	(10/26)
326 WOODCOCK (<i>Philohela minor</i>) Last seen.												
Sauk:.....	11/10	11/7	10/28	11/3	10/26	10/31	11/7	11/5	11/3	11/3
Dane:.....	10/31	11/12	11/14	11/7	11/13	11/9
327 LAKE WINGRA AT MADISON.												
Freezes over:.....	11/25	11/13	12/2	11/24	11/24
(Average date 1887-1895 was November 26. See Wing, p. 156.)												
328 LAKE MENDOTA AT MADISON. Record by U. S. Weather Bureau.												
Freezes over:.....	1/2	12/28	12/7	12/28	1/2	12/14	12/14	1/3	12/16	12/18	12/19	12/22
(Average date 1853-1940 was December 20. See Wing, p. 155.)												

STANDARDS AND TERMS, NOMENCLATURE

Averages based on less than four years are given in parentheses. Such averages are regarded as sub-standard, and are computed only to place the item in the chronological sequence. Incomplete dates, such as "by 3/1" are not used in computing averages.

Many dates for the Dane station are based on daily observations; few on less than tri-weekly observations. Most dates for the Sauk station are based on weekly visits.

Dates for events occurring between field trips are often interpolated by estimation, but only for such events as present evidence for estimating the probable date. The nature of such evidence is discussed later. Dates for bird arrivals, or for other animal behaviors, were never interpolated because they present no such evidence.

Blooming dates of plants are given in two ways. For plants without a perianth, the term "in pollen" is used, and means the dates between which pollen was found. In other plants, the term "in bloom"

means the dates between which a perianth was found. When only an initial date is available, the term "first bloom" is used.

A plus sign after a blooming date means that a few straggling blooms were observed beyond the closing date. Blooms on plants which have been mowed over, or in which bloom has been otherwise artificially deferred or renewed, are excluded. Thus weeds in stubble are artificially deferred by shading, while those in lawns or mowed roadsides are artificially renewed by mowing. Valid phenology in such cases must be taken from fencerows which have been neither shaded nor mowed. The equivalent of mowing occurs when insects sever the stems of wild lettuce (*Lactuca canadensis*) and Canada tick clover [279], or when deer decapitate *Veronicastrum* [236]. All these resprout, and the sprouts bear delayed blooms beyond the normal termination dates.

"Leafing" means the span of time from the bursting of the first leaf-buds to the completion of the

earliest leaves. Additional leaves of course continue to form as long as new growth continues.

The budding period is given only in a few plants which exhibit extraordinarily long budding periods, or in which the period varied greatly from year to year.

"Ripe" means that a fruit has colored, become edible, started to fall, or given other evidence of maturity. Fruiting phenology is shown under the item for bloom, except when the two are separated by many months (as in acorns and nuts).

In birds, the term "migrants arrive" means that some individuals commonly winter here, but the arrival date refers to individuals which seemed to be migrants. In species which do not winter, the term "arrives" is used without further specification.

The nomenclature of the following reference works is followed, except for some recent revisions:

Plants through June: Fassett's "Spring Flora of Wisconsin" (1938).

Plants beyond June: Deam's "Flora of Indiana" (1940).

Birds: Peterson's "Field Guide to the Birds" (1934). This guide follows the American Ornithologists Union Check-list.

Mammals: Hamilton's "The Mammals of Eastern United States" (1943).

Amphibians: Wright's "Handbook of Frogs and Toads" (1933).

Herbarium specimens of most plants of debatable identity have been filed either in the herbarium of Sara E. Jones, Bellaire, Ohio, or in the herbarium of A. Carl Leopold, 2222 Van Hise Avenue, Madison. A few residual items of debatable identity are asterisked in Tables 1 to 12.

Acknowledgments are gratefully made to Professors Norman C. Fassett, John T. Curtis, and H. C. Greene for checking many plant identifications, to Professor Kenneth J. Arnold for supervising the computation of standard deviations, and to James Zimmerman, now phenologist for the Arboretum, for many kinds of help both in field and office.

SELECTION OF ITEMS

Most of these records were collected as an incident to other field work. Experience has developed certain criteria for the selection of items which are "good" under these conditions. To illustrate these criteria, Tables 1 to 12 are drawn upon for examples, giving each its serial number. (Serial numbers appear in brackets, bibliographic references in parentheses.)

LABOR

A "good" item should not be too laborious. Thus horned owl nesting [2] and cardinal song [3] were detectable without labor, but during the same season it would have required tapping of trees to detect the first ascent of sap.

SHARPNESS

A good item should be sharp, in the sense that two observers looking for it will recognize and date

it alike. Thus the first cricket frog [25] is much more likely to be noticed than the first leopard frog [20] because the latter is silent on first emergence. Two observers could hardly avoid identical dates for cricket frog if they worked the same region, but they might well differ on the leopard frog.

In some items sharpness is a matter of adequate definition. Thus in breakage of ice in lakes [14, 22, 27] several days may separate the first break from the final dissolution, but when breakage is defined as "when one can row a boat across" the item becomes sharp.

Fortunately the bloom of most flowers is sharp, but in those grasses which do not extrude their pollen it is more difficult to detect first bloom.

Ripeness in fruits is sharp only when it coincides with falling, as in silver maple [26]. A wild grape is "ripe" on September 1 for jelly, but on October 1 for wine.

Some items are inherently difficult to define sharply. Thus in house-building by muskrats [319], variability in seeing or interpreting the evidence may exceed the year-to-year variability of the event.

This item is also beclouded by the fact that house-building dates differ by marshes, and this raises the question: how many marshes are represented in the record? It is feared that the record embodies little year-to-year consistency in this respect.

An occasional item is so sharp that it would be possible to record it to the nearest hour. Thus on August 18, 1946, Leopold found a single head of Indian grass [301] which had extruded a single stamen from its terminal flower. This was at 6:00 A.M. An hour later he happened to pass the same head and found it had extruded dozens of stamens.

COMMONNESS

The chance of detecting the first occurrence of an event, and especially of detecting it through a series of years, is obviously greater in a common species than in a rare one.

VISIBILITY OR AUDIBILITY

This specification is related to sharpness but is not identical with it. It often attaches to the observer, rather than to the plant or animal. Thus the nesting of horned owl is invisible to the unskilled observer, but is easily detected if one is working in an owl territory, and looks for the ears and tail of the incubating owl silhouetted above a nest. Incubation and first egg coincide in this species.

Likewise, the arrival of woodcock [18] is apt to be invisible to the observer without a bird-dog, and inaudible to the observer who is indoors during the "song" period at dawn and dusk.

The first call of the cricket frog [25] is an example of perfect audibility, but low visibility.

An example of perfect visibility is the ascent of the spring cankerworm [21], but the visibility depends on ringing an infested tree with tanglefoot.

When an event is difficult to see, cannot be heard, leaves no mark, and pertains to an uncommon

species, it becomes highly probable that the first occurrence is regularly missed. The record of emergence of Franklin ground squirrel [91] may be late for this reason.

RECURRENCE

Some otherwise good items do not recur yearly, and to this extent are poor. Thus horned owls did not nest in the Prairie du Sac observation area during four of the ten years covered. (See note after item 2.) Some orchids fail to bloom in some years. Fruits often fail to set by reason of frost, disease, or insect attack. Cankerworms by defoliating basswoods [233] prevented all blooming and fruiting at the Sauk station in 1944 and 1945. Most of the flowers of the bush clover [299] in 1946 were blighted by some unknown cause at the Sauk station, and in parts of Dane County.

In some items the question of yearly recurrence is confused and unanswerable at present. For example: do skunks [1] in this region hibernate with sufficient regularity to give validity to a series of emergence dates, such as those presented in Item 1? Albert Gastrow, who recorded the dates, is sure that they represent the emergence of the bulk of the skunk population on south slopes in his locality. Dens on north slopes emerge later. Individual skunks emerge sporadically during winter thaws, but never in such numbers as to becloud the main recorded date. It seems likely, from the literature, that these sporadic emergences are males, whereas the recorded dates include both sexes.

It seems possible that age, stored fat, and kind of winter dens (rock caves or burrows) may affect hibernation phenology. The dens on Gastrow's area are mostly caves in rock ledges.

CONTINUITY

Once an event occurs, it is a great advantage if it is continuous or recurs daily. All blooms have this advantage of continuity. On the other hand most animal behaviors (such as birdsong or the emergence of hibernators) are liable to be interrupted by bad weather, especially in early spring, or to occur only at limited hours.

The breaking of ice in rivers and lakes is, in effect, discontinuous when followed by refreezing.

EVIDENCE OF NEWNESS

The song of a bird carries no evidence of whether it has been going on for a day or a week, but a freshly opened flower among numerous unopened buds tells its own story. A sidewalk littered with fragments of squirrel-opened acorns [288], some fresh, others oxidized, tells its own story if the same sidewalk was clean a week ago.

Dates of events beginning between field trips cannot be interpolated without evidence of newness.

In an occasional instance, evidence of newness develops after the event, and one can check back on the date. Thus woodcock were first recorded at the Sauk station on March 16, 1946. This was nine days ahead of average, and the birds were silent,

as is usual on first arrival. Later Leopold found a nest which hatched on April 14. Allowing 20 days for incubation and four for laying, the first egg must have been deposited March 21. A blizzard on March 10-13 crowds the March 16 arrival from the other direction; hence its substantial accuracy is assured.

DISTANT FACTORS

Arrivals of migrant birds are likely to reflect distant as well as local weather. On the other hand, the behaviors of resident birds (such as song), and all developmental phenomena in plants, are inherently local. The break-up of ice in lakes is probably the best example of the cumulative effect of purely local factors. Other things being equal, locally-determined events are preferable as phenology items.

ABNORMAL ITEMS

In addition to the foregoing positive characters to be sought in phenology items, there are negative cautions to be observed in the acceptance of observations.

Bloom in dandelion [53] often occurs in March when the particular plant stands above a buried steam pipe, or hugs the south wall of a building. Such abnormal bloom is an interesting oddity, but poor phenology.

The development of plants on recently flooded areas is likely to be abnormal.

The bloom of stubble weeds, suppressed until mid-summer by the shade of the grain, and also the bloom of forbs cut off by insects or deer, have already been mentioned as abnormally late.

Some abnormalities are too rare to be important as phenology, but they are of interest as physiology. Puccoon [154] normally ceases blooming about July 1. In 1946 it ceased on July 6 at the Sauk station. But on August 5 a one-year-old seedling in a nursery bed bore two flowers, and on September 10 another bore one flower. No other seedling in the row showed any sign of blooming. The plants were only half the height of mature plants, and had only single stems. The writers have never before seen blooms on immature plants.

POPULATIONS VS. INDIVIDUALS

At least two variables, over and above weather, affect the phenology of plants: (1) the site variable, that is, differences in local environment, and (2) the genetical variable, that is, differences in response to the same environment due to different genetical constitutions in the individuals involved. A clear mental image of these two variables is essential to intelligent recording.

A developmental record for any given species, to be valid through a term of years, should either (a) embrace the entire gamut of site and of genetical constitution, or (b) it should be limited to certain individuals which have been selected in advance, and in which site and genetics remain constant. Alternation or mixture of the (a) and (b) types is fatal.

Most of the plant items embrace a wide range of

site and genetical constitution at the two stations. Unless marked (b), the record for any given item may be assumed to approach the (a) category. That is to say, items not specifically designated as (b) are supposed to span the period from the earliest bloom on the earliest site to the latest bloom on the latest site. This implies, of course, that the observer examines an equal variety of sites for each date for each year. Needless to say this ideal was not always carried out, but it usually was, especially for common species.

The choice between type (a) and type (b) is usually dictated by commonness. In some of the species, the population was too small for a record of the (a) category. Thus there is only one lilac bush [113] at the Sauk station. In such instances the record is marked (b) and an appropriate specification, such as "one bush" or "one clump" is added.

By and large, the (a) type is possible only for common species, while rare or locally uncommon species automatically assume the (b) type. The practical point is to reach a decision, and stick to it, in species of intermediate abundance.

In aquatic and bog plants, whole ponds or bogs sometimes display uniform earliness or lateness depending on the presence or absence of springs. For example:

	with springs	without
Skunk cabbage [28].....	3 / 20 / 45	about 4 / 10 / 45
Marsh marigold [71].....	about 4 / 10 / 46	4 / 15 / 46

For this reason a single specified pond or bog (phenology of the (b) type) is preferable for aquatics. A single water (Lake Chapman) was used for our Sauk records.

SOURCES OF ERROR

The foregoing discussion describes certain particular sources of error. There remain two more general questions:

(1) How much difference will occur as between two observers, looking for the same list of items in the same area, through the same years?

(2) How much difference arises from differing intensity of observation?

DIFFERENCE BETWEEN OBSERVERS

During parts of 1937, 1938, 1941, and 1942 Irvén O. Buss recorded phenology at Faville Grove, Jefferson County, 20 miles east of Madison. This is in the eastern end of the area defined as eligible for the Dane station. These records were not seen until he returned from military service in 1945. Upon comparison of his record with ours, 39 pairs of dates are found to be in common, covering 33 items during eight months of the year. Of the 39 pairs of dates, six are for birds, one for a mammal, and 32 for plants. The disparities classify as follows:

Identical with ours	13 pairs	33 percent
1-2 days difference	12 pairs	31 percent
3-4 days difference	7 pairs	18 percent
5-11 days difference.....	7 pairs	18 percent
	39 pairs	100 percent

The sum of all disparities is 101 days for 39 pairs, an average of 2.6 days each.

These disparities represent the error of observation plus any actual differences that may exist between the two localities. There is no available means for segregating these two components.

INTENSITY OF OBSERVATION

Animal Behaviors

The writers have become convinced that most animal behaviors in late winter are first exhibited by a few precocious individuals, and become general in the population by slow degrees. In 1946 some special records were kept to test this point. Many trained men, just returned from military service, enabled us to record not only the first occurrence of a behavior, but its gradual development. The following covers the combined observations of a dozen men afield daily on the University Campus and Arboretum.

Item	Species	Earliest Dates	Became General
3	Cardinal song.....	Jan. 5, 6, 9, 12, 13, 30	Feb. 17
4	Pheasant crowing.....	Jan. 10, 18, 30, Feb. 25	March 1
5	Marshhawk arrives.....	Feb. 16	Feb. 24
8	Chipmunk emerges.....	Feb. 8, 10, 18, Mar. 7, 8	March 14
23	Brown bat flying.....	Feb. 9	March 13
39	Ruffed grouse drums.....	Feb. 9	March 16
x	Garter snake out.....	Jan. 25, Feb. 17	Early March

The early dates for Items 3, 4, and 8 are believed to represent a slowly developing frequency; those for 5, 23, and 39 are believed to represent isolated early occurrences. In either case, a lesser intensity of observation would have yielded later "first dates," the degree of lateness and the selection of items depending on chance.

It is believed that this intensity-error in animal events diminishes rapidly as the season advances, and that it is never large in plant items, except in a few species to be discussed later. An intensity-error also probably exists in autumn animal items such as 316, 317, 319, 322, 324, and 326.

Bird Migration

Even if an event develops nearly simultaneously in a population, the chance of detecting its earliest occurrence depends on the number of observers afield. To explore the magnitude of this factor, the bird arrival dates of one observer are compared with those of 10 observers at the Dane Station.

For 16 years beginning in 1913, A. W. Schorger recorded the arrivals later published, as averages, in his "Birds of Dane County" (1929, 1931). He used only his own observations, and his skill as an ornithologist is nationally known. He was able to make few field trips during week days. His dates represent the best possible single-handed avocational effort.

Schorger's dates will now be compared with those gathered during the past decade by the writers and their collaborators:

Item	Species	Average Dates 1 Man	Average Dates 10 Men	10 Men Earlier by:
5...	Marshhawk.....	3/16	3/5	11 days
7...	Blue bird.....	3/11	3/9	2
10...	Redwing.....	3/11	2/28	12
16...	Canada goose.....	3/16	3/11	5
19...	Fox sparrow.....	3/24	3/21	3
36...	Field sparrow.....	3/30	3/20	10
	6 March birds, average.....			(7)
49...	Upland plover.....	4/18	4/16	2
55...	Towhee.....	4/13	4/7	6
64...	Brown thrasher.....	4/23	4/17	6
68...	American bitters.....	4/16	4/13	3
77...	House wren.....	4/30	4/22	8
	5 April birds, average.....			(5)
86...	Kingbird.....	5/4	5/1	3
87...	Crested flycatcher.....	5/7	5/3	4
95...	Baltimore oriole.....	5/5	5/3	2
96...	Warbling vireo.....	5/7	5/5	2
99...	Rose breasted grosbeak.....	5/7	5/6	1
103...	N. yellowthroat.....	5/8	5/1	7
106...	Wood thrush.....	5/9	4/28	12
112...	Whippoorwill.....	5/10	4/24	16
115...	Indigo bunting.....	5/11	5/10	1
111...	Scarlet tanager.....	5/9	5/9	0
122...	Catbird.....	5/6	5/2	4
124...	Nighthawk.....	5/14	5/6	8
	12 May birds, average.....			(5)
	23 Birds, March to May.....			5.6 days

Not all of the 15 observers covered all groups of birds, but it would be fair to assume that our dates are the earliest obtainable by 10 observers covering all groups, and less confined to week-ends than were Schorger's. The span of years reported in the present study is shorter, but both spans seem to be long enough to avoid distortion by exceptionally early or late seasons. The five day difference is believed to represent the greater intensity of the ten-man effort.

Plants

In flowering spurge [196] the first blooms are borne singly, and are so inconspicuous, as compared with the later massed corymbs, that one must learn to look for them. During the process of learning, they are likely to be overlooked. The result is that in a series of annual records, the early years are likely to show dates which are later than they should be.

There are some plants in which the very earliest blooms are perfectly visible, but they occur on so few individuals that they are likely to be overlooked. This group includes hedge bindweed [205], chicory [218], bull thistle [282], white snakeroot [293], greater ragweed [295], lesser ragweed [293], *Liatris spherioidea* [300], and Canada goldenrod. These species are put in the variable category because the records definitely sustain it. In addition, it is the impression that all asters, oaks, hickories, poplars, and willows likewise display wide variability, including a small proportion of especially early individuals.

The very early individuals probably represent

genetical, rather than environmental, variations for the following reasons:

(1) In annuals like the ragweeds, extra early plants have never been found twice in the same place.

(2) In white snakeroot, at both stations, the very earliest blooms for three years have occurred at two particular spots, both on a north slope and shaded. The two sites would seem to be cold rather than warm.

(3) In chicory, at the Dane station, the earliest bloom for the last three years has occurred at a particular spot on a north slope which seems cooler than the usual "curbstone" habitat of this species.

(4) In willows and sumac earliness and lateness seem to show a clonal distribution. At the junction of two clones one can see wide disparity in earliness on identical sites.

TOWN VS. COUNTRY ERROR

It was suspected that in spring plant development in urban habitats is commonly earlier than in rural ones. To test this belief, Donald R. Thompson kept records on 15 plants common to Madison and the University Arboretum, spanning the period March to May, 1946. He found that 13 of the 15 species were earlier in Madison:

Days Earlier in Town

9 forbs.....	2, 1, 11, 8, 0, 4, 6, 0, -3 days
6 woody plants.....	2, 2, 2, -1, 6 days
Average	4 days

Thompson's data are certainly not conclusive, but they are consistent through March and April, the first instances of earlier rural bloom appearing in May.

Until 1944 no conscious effort was made to avoid recording a plant in town one year, and in the country the next year. The bulk of our plant records are therefore subject to this error. It cannot, however, affect items of the (b) category (fixed stations), nor can it affect plants found only in the country, such as prairie and marsh plants. It is most likely to affect wild flowers in gardens and trees on lawns or streets.

FORM OF RECORDS

Phenological errors can be greatly reduced by a form of record which automatically reminds the observer, while in the field (not afterward), what current items are likely to terminate, and what new items are likely to develop, on the date of any field trip. Without such an automatic reminder, the observer is less likely to detect the earliest occurrence of new items, and termination dates are likely to be overlooked entirely. The automatic-reminder type of record was begun in 1939. Even with the best of records, terminal dates are usually cruder than beginning dates.

GENERAL DISCUSSION OF ERRORS

The following net conclusions can be drawn from the foregoing discussions of errors and of the peculiarities of phenological data:

(1) Any given aggregation of data is subject to numerous possible errors, only part of which can be identified.

(2) The more species, the more years, the more stations, and the more observers behind any given deduction, the greater the chance that errors will compensate.

(3) During the decade here treated, the degree of error declines progressively.

(4) Phenology of the (b) type (fixed stations) avoids some errors.

(5) Caution is necessary in attaching significance to differences of small magnitude.

PLANT GROUPS

Those who work with soil, crops, wild plants, wild animals, or landscapes sometimes wish to know what plants may be expected to be in bloom, or in fruit, at a given time. For their convenience such data have been segregated in diagrammatic form, in Figures 1, 2, 3, 4, and 5. These assemblies present an average of the two stations, and ignore deviations due to early or late years. They include some

species which are omitted from Tables 1 to 12 because the record is too short.

The point of each arrow is the beginning date, and the length of the arrow is the duration of the event.

By projecting a vertical line through any given date, the reader can tell at a glance what species are likely to be in bloom (or in fruit) on that date.

It is perhaps of interest to note that all four groups of flowers describe, in their succession of "arrow points," a reversed "S" curve. The groups differ only in the degree of curvature, and the dates of inflexion. Woods flowers inflect in May, prairie and sand plants and weeds in June (with some minor undulations) and marsh plants in July. The shape of these curves is of course affected somewhat by the local assortment of sites and species, and by the degree to which all are covered.

WOODS FLOWERS

Figure 1 assembles some of the wild flowers characteristic of oak-hickory, climax hardwood, and oak-jack pine woodlands at their point of confluence in this region.

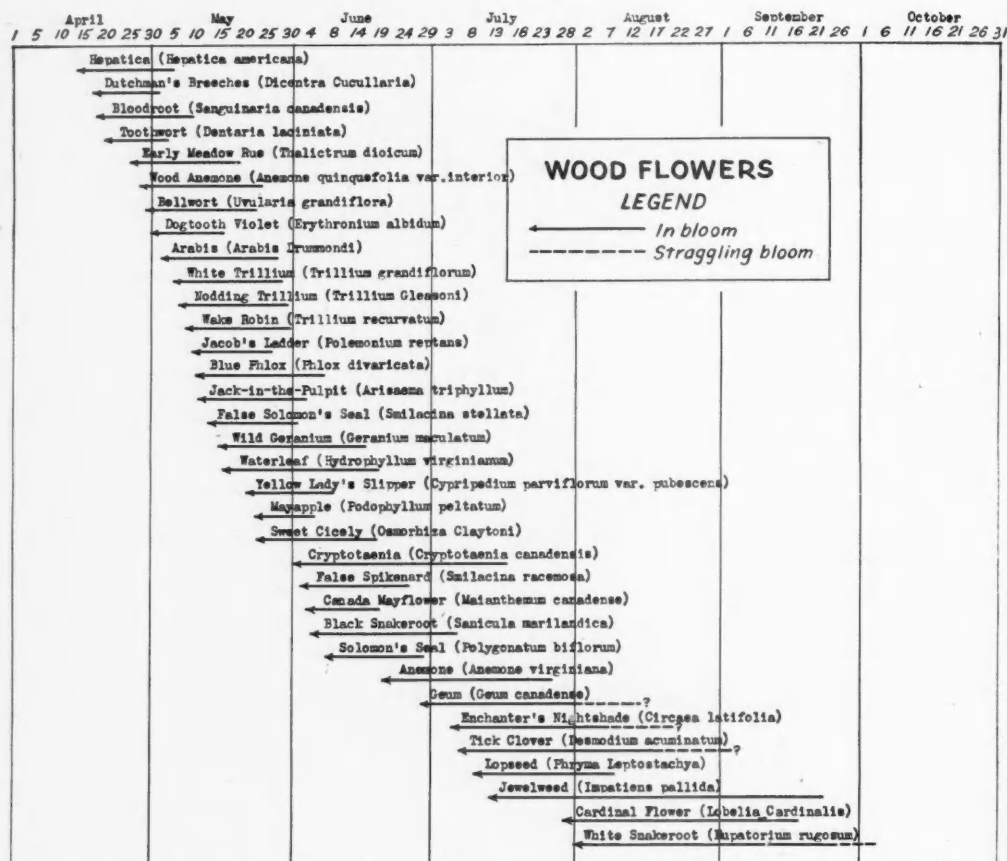


FIG. 1. Average Blooming Periods of 34 Woods Flowers.

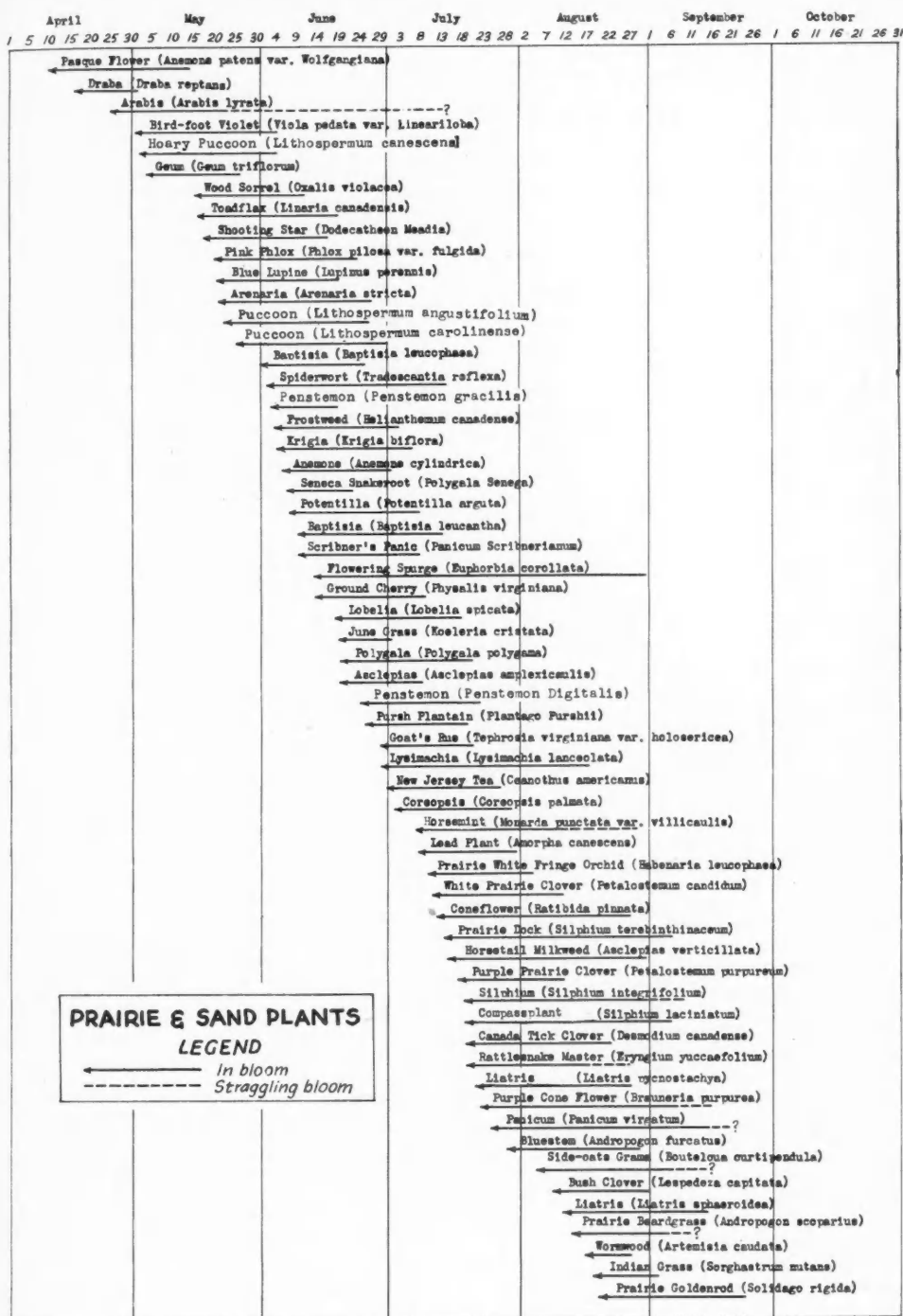


FIG. 2. Average Blooming Periods of 59 Prairie Plants and Sand Plants.

A conspicuous character of this group is the early bloom and short duration of bloom in the first 21 species. Their average duration is 21 days. These species bloom before the leafing of trees is complete, and thus contrive to receive at least partial sunlight, even when occupying sites shaded by overhead trees, and often by a shrubby understory as well. That this short early bloom is actually an evolutionary adaptation for seizing sunlight is sustained in some species by the fact that the leaves turn yellow and die as soon as fruiting is completed. For example, the leaves of Dutchman's breeches and dogtooth violet are yellow by the end of May and dead by mid-June. This early death occurs even in transplanted individuals with plenty of light and moisture. The yellowing foliage of these two species is the earliest "fall color" of the year.

PRAIRIE AND SAND PLANTS

The average blooming dates of 59 forbs and grasses are assembled in Figure 2. Of the 14 flowers which bloom before June 1, nine are confined to hot dry sands and gravels. On such sites, in very drouthy springs, snow water is the only moisture likely to be available. *Pasque* [44] and *Draba* [51] are examples of sand plants which can bloom on snow water.

In some early sand flowers, the blooming period is short regardless of the weather; thus *Draba* did not span more than two weeks in any year. Other early species are opportunist; thus *Arabis lyrata* [74] bloomed from April 11 to June 6 and straggled to August 12 during the cool spring of 1945, whereas in normal years it ceases to bloom in May.

Some prairie grasses and forbs start the season's growth very late. Could this be an evolutionary device for avoiding damage from spring fires? For example, bluestem [290] grows no visible leaves until late May, whereas most other perennial grasses become green in April. Butterfly weed [241] does not sprout until June 1, whereas the other milkweeds sprout a month earlier.

The prairie group is peculiar in its interspersions of long and short blooming plants. Its long collective span, together with the tendency of prairie grasses to color in fall, gives it great value in wild landscaping. Every month from April to October offers something to see on a prairie.

WEEDS

The average blooming dates of 46 common weeds are presented in Figure 3. As has often been pointed out, there is no objective definition of the term "weed," and none is claimed for Figure 3, except that it includes plants which somebody, for some reason, dislikes. The group might well be larger: thus Asiatic honeysuckle [123] is probably a greater threat to the native flora in this region than any weed in Figure 3, barring quack grass [197]. Of the 46 species, not more than half a dozen are dangerous in the sense of usurping land that has not been abused. Most Wisconsin weeds are objectionably abundant mainly in overgrazed pastures [239,

255, 259, 282, 289, 298, 307], and are preferable to the erosion which would be augmented by their absence. Winter animals are largely dependent on weed seeds.

The exotic perennials which comprise the bulk of the weed list have certain phenological characters in common. First, their period of bloom is long. The average duration, exclusive of straggling, is 45 days. By reason of straggling, the termination of bloom often lacks sharpness. Second, they commonly resprout and rebloom after mowing, and also after interruption of bloom by drouths. Examples: [53, 182, 255]. Some display straggling blooms even when not interrupted by mowing or drouths. Many straggle until frozen. Examples: [177, 218, 255].

HAYFEVER WEEDS

There is a discrepancy between the development of pollen in the two ragweeds at the Dane station, and the detection of aerial pollen by the Allergy Laboratory of the Wisconsin General Hospital. In two of the last three years the hospital has detected pollen in the air before any phenologist could detect general bloom in the field.

There is also a discrepancy between first general bloom in ragweed, and first pollen in a few precocious plants. In two of the last three years one or more precocious individual plants have been found, by accident, far ahead of the general population:

First Pollen	Precocious Plants	General Population	Allergy Laboratory
1944.....	x	7/30	7/28
1945.....	7/13, 8/1 (both lesser)	8/7	8/1
1946.....	7/26 (greater)	7/31	7/31
Average difference.....	15 days.....	3 days	

The question is: does the earliest pollen detected by the Allergy Laboratory originate in other regions, or does it originate in these precocious local plants? The present data yield no clue.

The precocious plants are very scarce, and are doubtless genetical aberrations. Three years' search has yielded only the three plants.

The average Dane County dates (August 5 for lesser and August 8 for greater ragweed) are later than the August 2 average for both species in this region given by Wodehouse in "Hayfever Plants" (1945).

MARSH PLANTS

The average blooming dates of 28 marsh plants are presented in Figure 4. This group consists, in large part, of conspicuous abundant perennials with long blooming periods (average duration 38 days). As in the prairie group, the collective span of bloom includes the entire growing season.

As already pointed out, the date of first bloom in early marsh species is strongly affected by the presence or absence of springs.

Some marsh plants have highly specific animal relationships. Robert A. McCabe (unpublished) has found that the alder flycatcher in the University Arboretum uses the dry stalks of *Angelica* [160] as a territorial perch, and the shredded bark of the

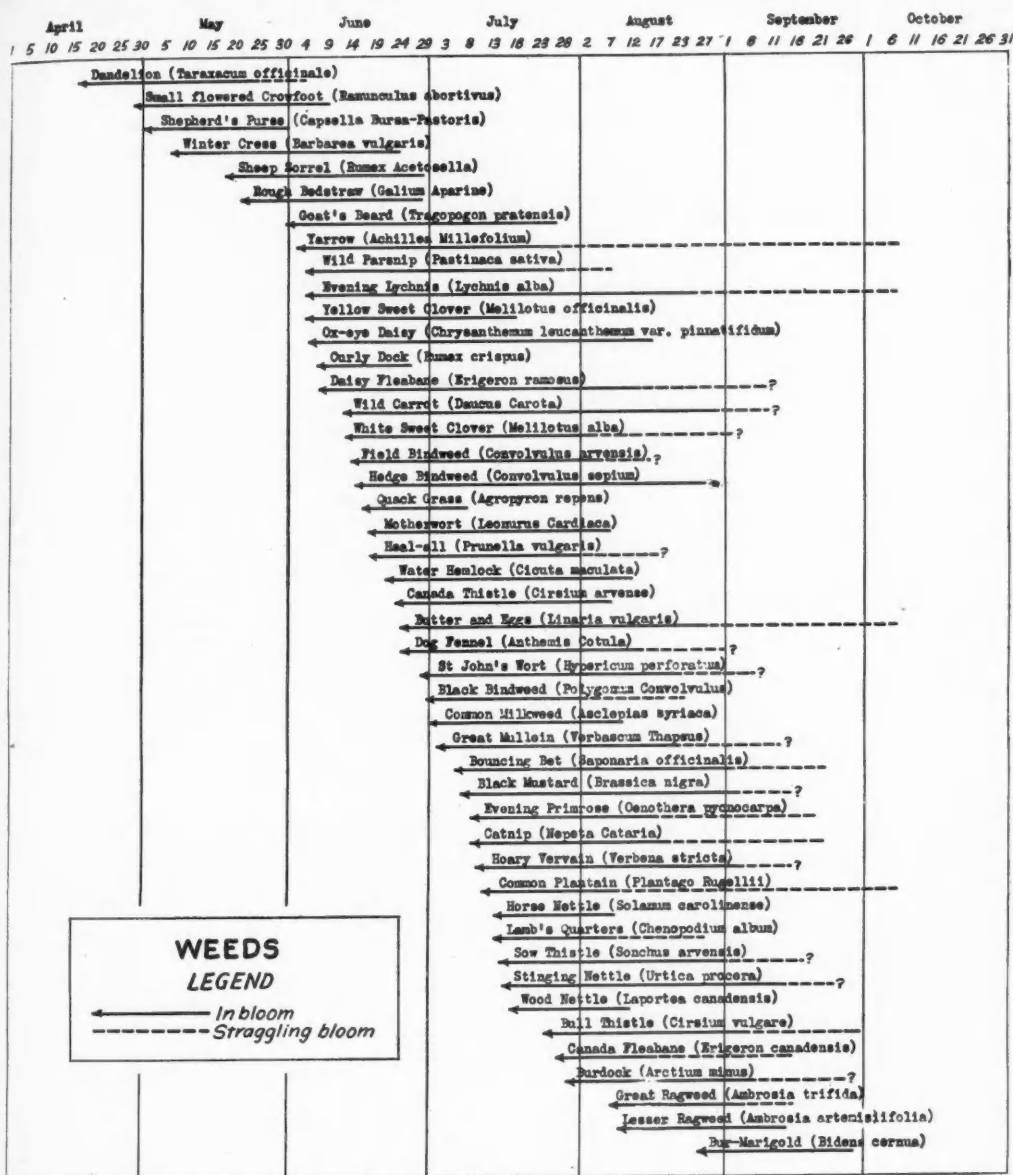


FIG. 3. Average Blooming Periods of 46 Weeds.

swamp milkweed [244] as his principal nesting material. The milkweed becomes "shreddable" only after spring sun and wind have loosened the dead bark, hence the relationship is conditioned by phenology. McCabe suspects that the flycatcher's food supply, during the critical weeks of the nesting season, hinges on the insects attracted by concurrent marsh blooms, and that shade for nestlings is tied in with the leafing phenology of the elder and red dogwood bushes in which most nests are

built. Such plant-animal dependencies, partial or complete, are doubtless the rule rather than the exception, but few have been explored by research.

WILD FRUITS

A chronology of 27 wild fruits, arranged in order of first ripening, is presented in Figure 5. The blooming periods are also given. Species without known food value, such as wahoo [203], are omitted. Falling periods are indicated by dashed bars; inde-

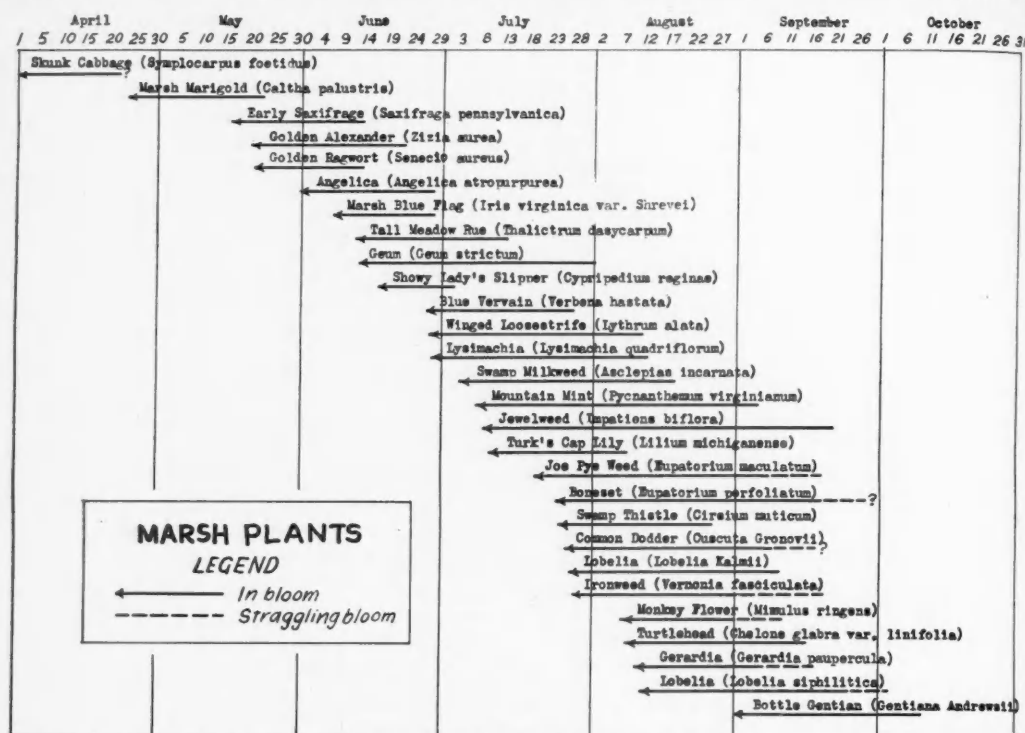


FIG. 4. Average Blooming Periods of 28 Marsh Plants.

terminate fallings after November 1 by plus signs, or by adding terminal dates of falling.

These 27 fruits differ greatly in their ripening phenology, and in the degree to which they are consumed by animals.

Thus among mast fruits, all oaks fall as soon as they are ripe; walnuts adhere to the tree until frost; hazelnuts do not fall, but are gradually removed by mice and chipmunks. Burr oak acorns in the city of Madison are in most years completely consumed by squirrels [see Item 288] a month before ripening; to get the date of natural fall one must search fence-row oaks in rural areas where squirrel pressure is less intense.

Juneberries at the Sauk station are completely consumed by orioles as soon as they turn red, and before they are ripe. Hence it is impossible there to record the duration of ripe berries on the tree. Grey dogwood berries are consumed or knocked off by robins by late October.

On the other hand, the proportion of the blackberry, dewberry and elderberry crop consumed by animals seems very small in this region.

Of the fruits which adhere to the tree after November 1, some fall or are consumed gradually (grape, nannyberry) while others may be ignored until spring, and are then obliterated in two or three days by cedar waxwings (mountain ash).

The maximum variety of ripe wild fruits is available about September 1.

Table 5 may be useful for planning a sequence of fruits for wildlife, or for determining the best date for gathering wild fruits for eating or preserving. The table is deficient in the phenology of edible mushrooms, for which no records were kept.

ANALYSES

In the pages which follow, six sample analyses are given of the data in Tables 1 to 12. The purpose is exploratory; to show that analysis is possible, and if sound may shed light on a wide variety of questions. The number of questions is probably limited mainly by techniques. The writers have no illusion that their techniques are the best.

Most analyses depend on comparisons with averages, means, or norms. It is of the utmost importance to realize that the biota never conforms to averages. The only physical meaning of an average is that the deviations from it should equalize. Significance inheres mainly in the frequency and amplitude of the deviations.

YEAR TO YEAR VARIABILITY OF SPECIES

As a means of visualizing the year-to-year deviation of plant and animal species from their own averages, the longest series of dates from Tables 1 to 12 are presented graphically in Figures 6 and

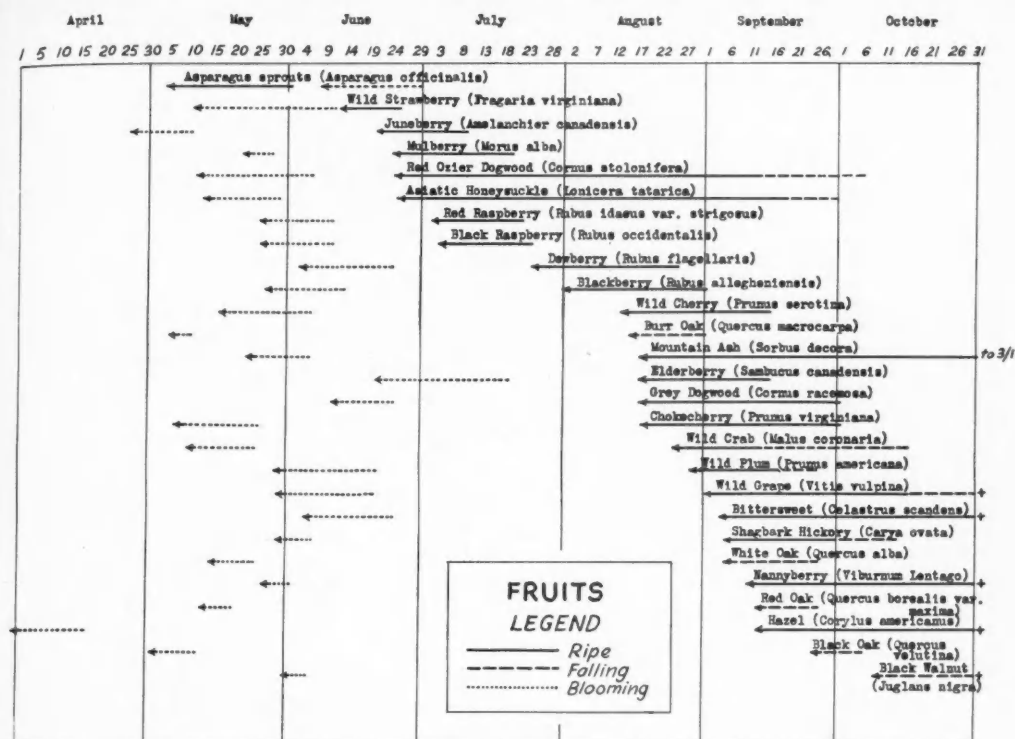


FIG. 5. Average Blooming Dates and Periods of Ripeness in 27 Wild Fruits.

7, in groups by months. Points above the baseline represent lateness (plus deviation); points below the baseline represent earliness (minus deviation).

Visual inspection of Figures 6 and 7 suggests that there is a seasonal decline in deviation, the early spring curves being more "turbulent" than later ones. At any given season, some species seem more "turbulent" than others.

In order to arrive at some measure of turbulence, "estimated standard deviations" were computed for each of the species. The deviation, in days, is entered under each species name (for instance in skunk, $s = 17.0$ days). The formulae used to compute one station, two stations, or averages of several species will be supplied on request.

DECLINE IN DEVIATION

To test the existence of a seasonal trend in the variability of items, the deviations of all the animals and plants shown in Figures 6 and 7 are averaged by months as follows:

	28 Animals	20 Plants	Both
February-March.....	10.3 days	x	10.3 days
April.....	8.9	9.5 days	9.2
May.....	6.8	6.3	6.7
June.....	x	7.0	7.0
July-August.....	x	6.7	6.7
April-August.....	8.6 days	7.4 days	8.1 days

A progressive decline in variability is clear in animals from February up to the end of bird migration in May, after which there are no data. Plants decline during April and May, but there is no large difference between months after May.

The lumped data for both plants and animals show a progressive decline from February to May, followed by a relatively stable period. The net conclusion is that from February to May, inclusive, the year-to-year "turbulence" of animals and plants diminished by nearly half.

LENGTH-OF-DAYLIGHT SPECIES

A few birds in Figure 6 and a few forbs in Figure 7 are conspicuous for close adherence to their own averages. Their deviations compare as follows with the average of other species during the month in which each occurs:

Item	Species	Month	Deviation	Average Deviation of others in same month
49	Upland plover.....	April	3.2 days	9.1 days
95	Baltimore oriole.....	May	3.6	8.4
96	Warbling vireo.....	May	3.8	8.4
99	Rose-breasted grosbeak.....	May	3.1	8.4
103	Northern yellowthroat.....	May	3.8	8.4
114	Indigo bunting.....	May	4.4	8.4
6 birds above, April and May.....				3.7 days
13 other birds, April and May.....				8.7 days

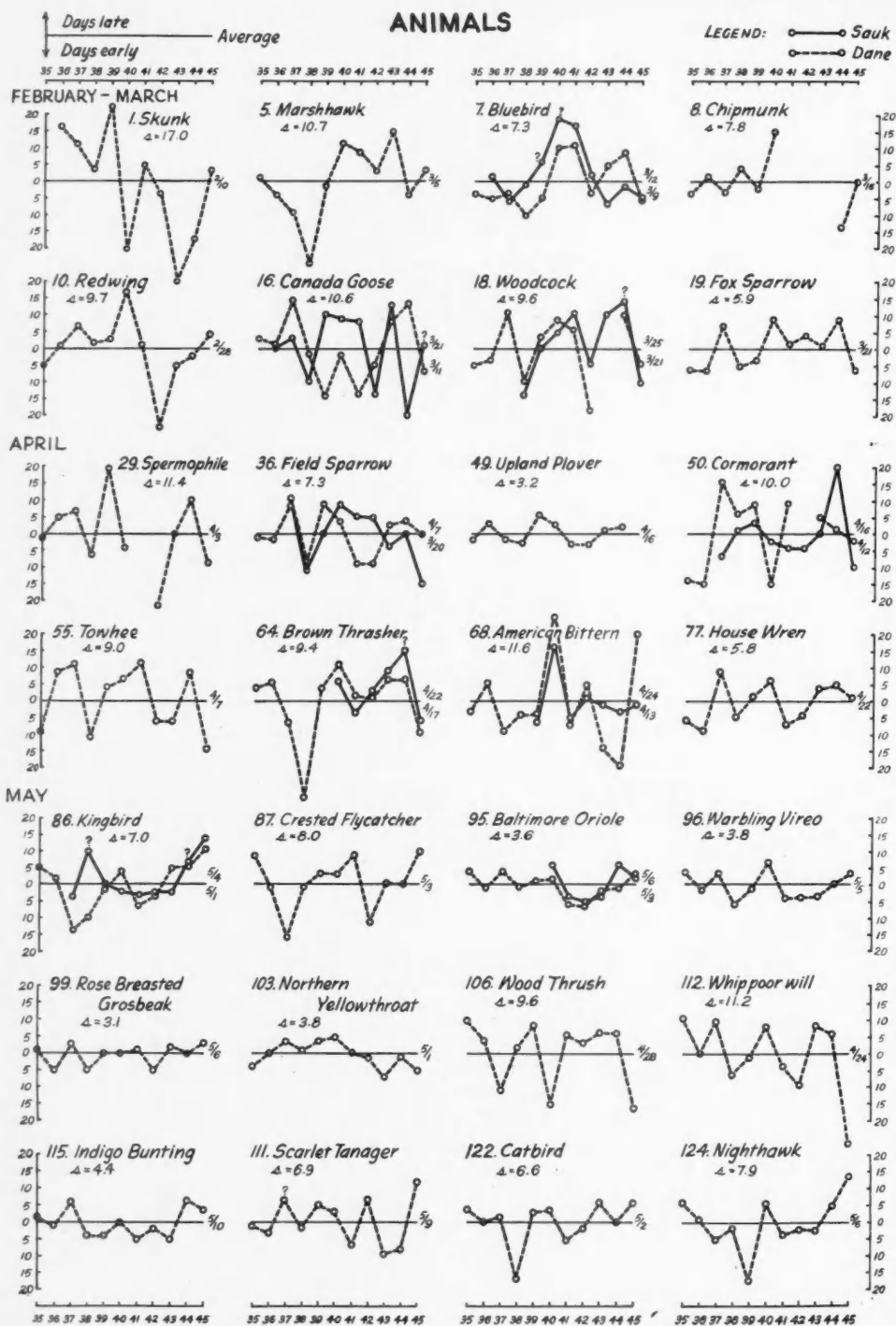


FIG. 6. Deviations from Average Dates in the Emergence or Arrival of 28 Animals, 1935-1945.

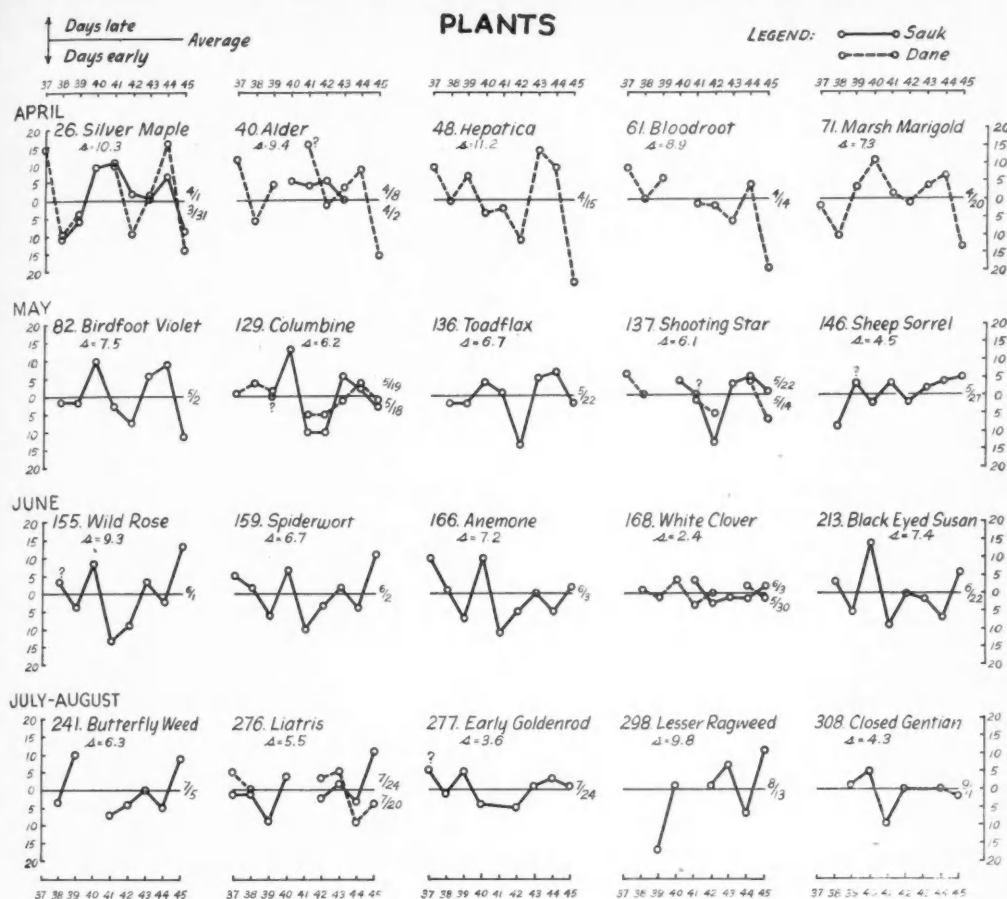


FIG. 7. Deviations from Average Date of First Bloom in 20 Plants, 1937-1945.

It is clear that in these six birds the deviation from their own average arrival date is less than half that characterizing other birds arriving during the same month.

Deviations in four non-turbulent forbs are compared with other plants blooming during the same month as follows:

Item	Species	Month	(Sept. 1) Deviation	Average Deviation of others in same month
146	Sheep sorrel.....		4.5 days	6.6 days
168	White clover.....	May	2.4	7.6
277	Early goldenrod.....	June	3.6	5.9
308	Closed gentian.....	July	4.3	x
4 forbs above, May-August.....			3.8 days	
11 other plants, May to August.....				7.3 days

In these four forbs the deviation from their own average blooming date is a little over half of that prevailing in other plants during the same month.

That some plants are governed primarily by length-

of-daylight, as distinguished from other factors of current weather, is by now a familiar concept. The phenology of these four forbs suggests that day-length is a heavier component in their timing mechanism than in that of other contemporary plants.

The six birds present a somewhat more puzzling case, for all of them winter in the tropics, where differences in day-length are much reduced. The plover, of course, winters beyond the tropics, where the seasons are reversed. One can only conclude either that very small changes in day-length suffice to move them, or that there is some seasonal rhythm controlled by some other force.

Of the 19 birds and 15 plants appearing in Figures 6 and 7, white clover deviates least (2.4 days), and is also probably one of our most reliable records. Its wide distribution and abundance makes for accuracy in detecting first bloom, and when bloom starts in a single plant, the whole population soon follows.

It seems clear to us that, given enough data, both

plants and birds could be graded for year-to-year variability, and that such a gradation might throw light on the biological distribution of physiological timing mechanisms.

THE CHARACTER OF SEASONS

Visual inspection of Figures 6 and 7 shows that certain years were prevailing early, or late, during certain months. Thus most birds and plants were early in 1938 up to May. Again in 1940 birds were late through April, and plants through June. This whole question will now be discussed in detail.

Each event has a normal or average date, from which it deviates from year to year according to the earliness or lateness of the season. This being true, the character of a season can be expressed by a succession of deviations in its events through its component months. In Figures 8 and 9 the character of two seasons, 1944 and 1945, is thus expressed. Each has two graphs, A and B, in each of which the horizontal baseline represents average or normal date.

In the A graphs the actual dates of about 280 events are plotted as deviations above or below the

baseline. An event earlier than average is plotted below (minus deviation); an event later than average is plotted above (plus deviation). Symbols differentiate animals from plants, and also the two stations.

In the B graphs the deviations are averaged, for each five-day period, for plants and animals separately. These average curves appear against a stippled background of current temperatures, likewise expressed as the net deviation from average during each five-day period. In these temperature graphs, minus deviations (in degrees Fahrenheit) are colder, hence they are plotted above the baseline to correspond with lateness in phenology. Thus if the mean temperature for five days deviated from normal by -12° , -10° , -5° , $+5^{\circ}$, and -1° , the period is plotted as deviating $-28 + 5 = 23$ degree-days above the baseline.

Curves of cumulative temperature deviation, in terms of degree-days, were tried as an addition to the B graphs, but they did not seem to explain anything, and hence are omitted. Cumulative curves are not dismissed as of no value, but it is believed that

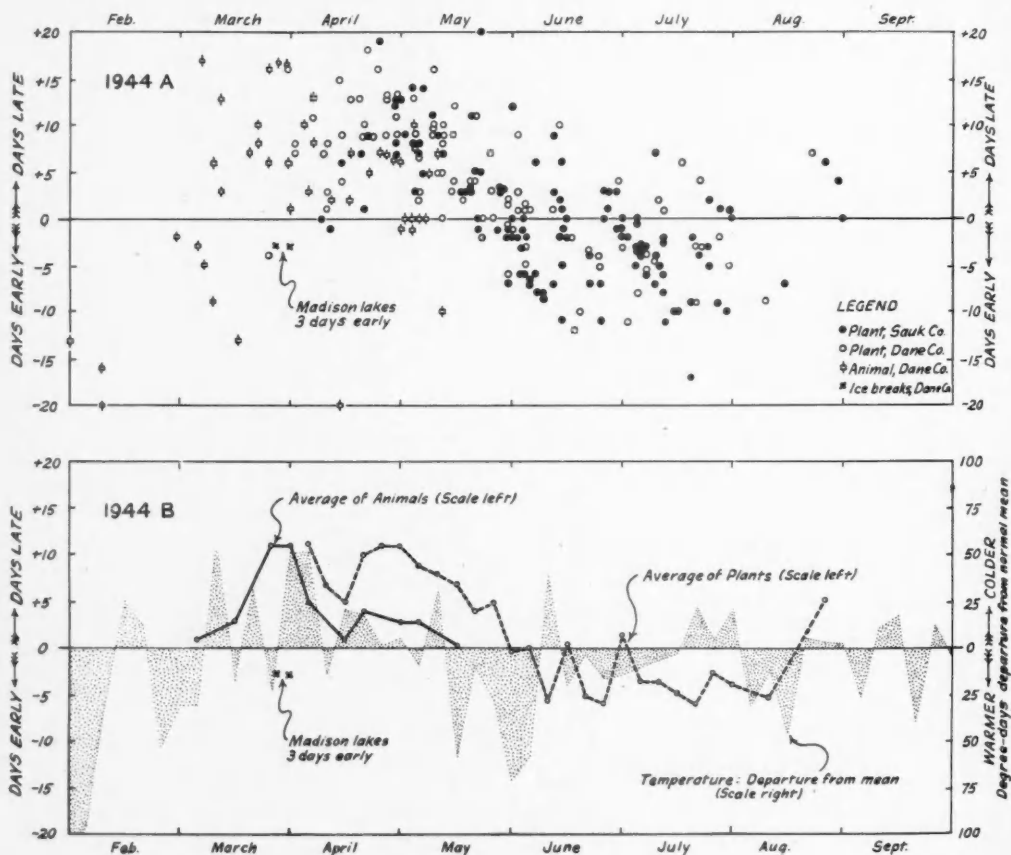


FIG. 8. (A) Deviations from Average Date in 280 Plant and Animal Events in 1944. (B) Average Deviation of Animals (solid line) and Plants (dashed line) in Relation to Temperature (Stippled).

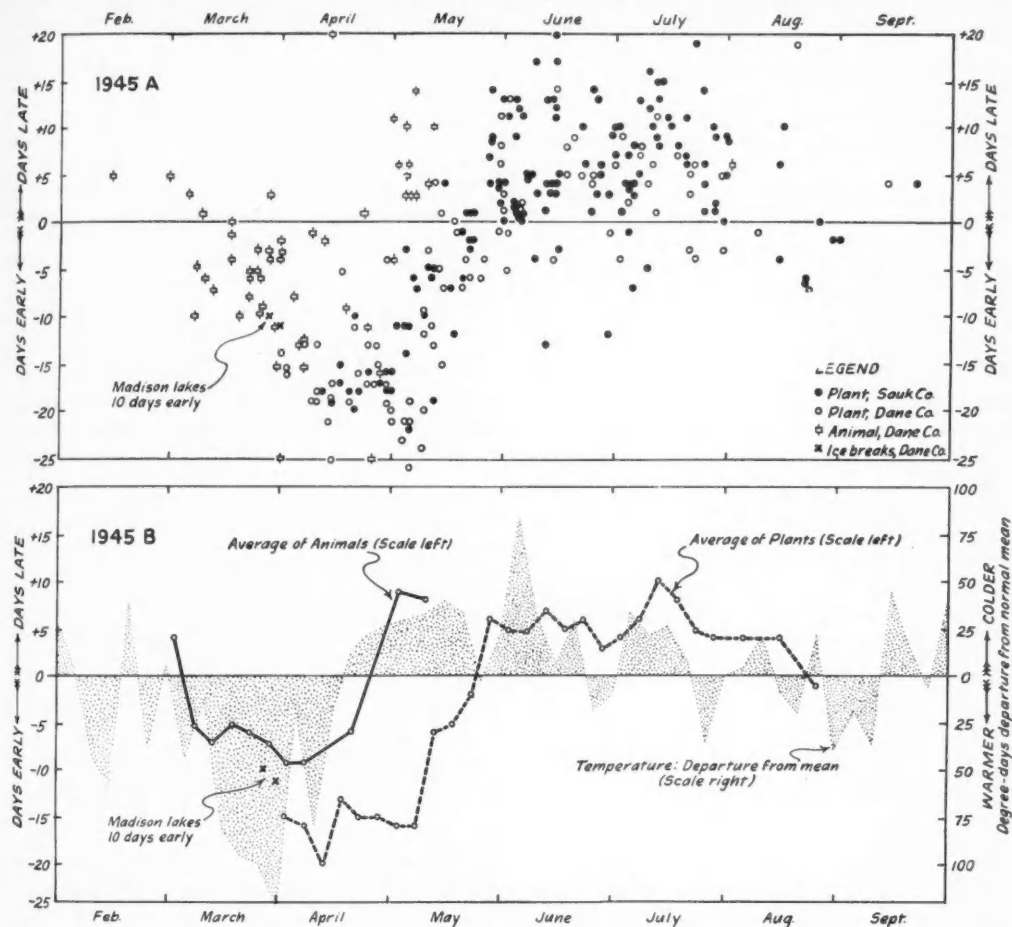


FIG. 9. (A) Deviations from Average Date in 280 Plant and Animal Events in 1945. (B) Average Deviation of Animals (solid line) and Plants (dashed line) in Relation to Temperature (Stippled).

accumulations must relate to some threshold temperature. Zero Fahrenheit is a meaningless threshold, especially for plants.

Precipitation curves are omitted from Figures 8 and 9 because both years were normal except for a wet June in 1944 (+2.62"), and a dry July in 1945 (-1.74"), and a dry October in both years (-2.19", -2.04"). The net deviation for the year was +0.13" in 1944 and -3.52" in 1945.

The term "phenograph" is suggested as a short name for such seasonal summaries as are presented in Figures 8 and 9.

INTERPRETATION OF PHENOGRAPHS

Several precautions were observed in preparing Figures 8 and 9. Items with averages based on less than four years are omitted. Sauk animals are omitted because of the possibility, already discussed, of late dates.

Autumn items representing the onset of winter are omitted, because the terms "early" and "late"

then have meanings opposite to their meaning in spring. It should be noted that each item is plotted perpendicular to its average date.

When the weather changes (stippled area crosses the baseline) the response to the change is subject to a lag, and the extent of the lag is the horizontal distance from the weather crossing to the plant or animal crossing.

Of the two seasons here presented, 1944 approached normalcy in both weather and phenology, while 1945 was abnormal in both.

PHENOGRAPH FOR 1945

After a normal winter, 1945 opened with an extraordinarily warm March and early April. During the period March 1 to April 13, all but four days were warmer than normal. Temperature deviations ran as high as 28 degrees on single days, and for five-day periods as high as 125 degree-days.

On April 14 the weather turned from warm to cold. It remained abnormally cold through the

remainder of April and May, June, and July. During this 77 day period, all but 17 days were colder than normal. Normal temperatures did not reappear until August and September. There was no drouth to mask the effect of abnormal temperatures.

In short, 1945 was a "self-recording experiment" in which more than 50 animals and 100 plants at two stations registered their responses to a mid-April shift from warm to cold. Average dates for other years provide the "control."

During the early spring warm spell, migratory birds arrived earlier and earlier until the weather changed, at which time most birds were appearing 5 to 15 days ahead of schedule. The onset of cold brought a rather prompt change to lateness; there were no early bird arrivals after May 1. The many species due during the first ten days of May were all from 2 to 14 days late.

In strong contrast to this prompt response of birds to the mid-April shift in temperature, plants responded much more slowly. No plants were late until mid-May, a month after the onset of cold. Maximum lateness did not develop until mid-June, two months after the onset of cold. The average curve for plants crosses the baseline 29 days later than the average curve for animals. Apparently the developmental mechanism in plants set in motion by the early warm spell gathered a momentum which expressed itself in early bloom through a month of ensuing cold.

So far 1945 phenology has been discussed in terms of plants as a whole and animals as a whole. The

behavior of particular species during the warm and cold periods will now be considered.

Table 13 presents the items normally occurring during the warm period March 5 to April 13. These are classified by groups in a time sequence. It is apparent that the warm period produced the greatest earliness in forbs and woody plants, the least in birds and mammals, with lakes in an intermediate position. It is of some physiological interest that subterranean mammals like moles and spermophiles should have been early at all. The number of mammal items is, however, too small to be conclusive.

Table 14 is a condensed summary of the cold period, April 14 to July 27. The left hand number of each pair is the number of items early or late; the right (in parentheses) the average number of days early or late. It is apparent that earliness in birds and mammals ceased in mid-May, a month after the onset of cold weather, but that it persisted in some forbs into July. Woody plants, on the other hand, lost their momentum by the end of May. The impact of cold was very unequal as among species, as evidenced by the simultaneous existence of early and late groups, especially in forbs during late May, June and July.

It should be realized that some of the forbs persisting in earliness long after the onset of cold were *still underground* when the cold hit. Thus white trillium [104] bloomed May 1 and April 15 at the two stations, six and 20 days early. It did not emerge from underground at the Sauk station until April 14, a day after the cold began. In short, momentum-earliness was *in the root*.

TABLE 13. The Warm Period, March 5-April 13, 1945.

Normal Date	Birds	Mammals Amphibians	Forbs	Woody Plants	Lakes and Rivers
March 5-15	Bluebird 6 Meadowlark 1 Robin 2 Killdeer 15	Woodchuck 1			
March 16-25	Grackle 10 Dove 6 Woodcock 4 Fox sparrow 6 Cowbird 3	Chipmunk 0 Mole 8 Leopard frog 3			Wisconsin River . . . 6 Lake Wingra 10
March 26- April 5	Field sparrow 3 Phoebe 13 Kingfisher 8 Sapsucker 4 Hermit thrush 15 Purple martin 2	Bat 15 Cricket frog 9 Spermophile 8		Silver maple -8, -14	Lake Mendota . . . 12
April 6-13	Towhee 13 Cormorant 2		Pasque 18, -12	Pussy willow 13 Hazel 15 Alder 16 Aspen 18 Forsythia 17 Cottonwood 22 Elm 19, -19	
Average earliness:	- 6 days	- 6 days	-15 days	-14 days	- 9 days

TABLE 14. The Cold Period, April 14-July 27, 1945.

Period	Birds		Mammals and Insects		Forbs		Woody Plants	
	Early	Late	Early	Late	Early	Late	Early	Late
April 14-20.....					6(17)		1(17)	
April 21-30.....	5(12)	1(20)	1(11)		9(16)		4(15)	
May 1-10.....	1(5)	8(5)		1(6)	12(16)		11(16)	
May 11-20.....		3(10)			12(11)	2(2)	4(7)	1(4)
May 21-31.....					5(5)	5(5)	1(6)	3(7)
June 1-14.....				2(1)	3(4)	12(6)		8(9)
June 15-30.....					1(12)	9(6)		6(9)
July 1-14.....					3(3)	25(8)	2(4)	3(9)
July 15-27.....				1(8)	3(2)	13(6)		2(8)

PHENOGRAPH FOR 1944

In 1944, temperatures displayed a succession of short, mild deviations from normal, much less sustained and less radical than in 1945. March and April were somewhat cold, May and June somewhat warm, the shift from cold to warm occurring on May 12. However, neither of these major periods was intense enough, or free enough from temporary reversals, to allow one to feel sure just which change in temperature produced any given deviation in phenology.

In this climate, these short mild frequent deviations in weather define normality.

In 1945 March birds changed quickly from lateness to earliness in response to warmth; in 1944 they changed quickly in the opposite direction.

In mid-April both animals and plants returned very briefly to near-normal dates, for reasons not clearly visible in the temperature graph. It is possible that birds were responding to the brief warm spell in early April, and plants to the preceding one in late March, which also opened the lakes.

Early May birds were back to normal before the weather turned warm; the antecedent cold was evidently too mild to retard them.

The emerging mammals in 1944 show the same response to current weather as in 1945 (Table 13), but only three species are of record:

	Deviation	5-day temperature deviation
Woodchuck.....	— 9 days	+50°F.
Chipmunk.....	—13 days	+30°F.
Spermophile.....	—10 days	+10°F.

The clearest fact in the March-May segment of 1944 B is the lag of plants behind animals after the shift to warm weather on May 12. The plant curve crosses the baseline on June 1, 15 days later than the animal curve, and 19 days later than the general change to warm weather.

The plant record for 1944 was analyzed by species, as in Table 13, for behavior following the general change to warm weather on May 12. The analysis discloses less decisive responses, and no point of interest not already discussed, hence it is omitted.

COLD, FROST, AND SNOW EFFECTS

It is well known, but perhaps not often enough emphasized, that winter animals, whether active or

hibernating, are subsisting on last year's solar energy, stored either as living prey, body-fat, seeds and fruits, or bark and buds. Winter phenology reflects only the rate and manner in which these stored materials are drawn upon. As already pointed out, the winter items show extreme deviation in date. This may be due not only to fluctuating weather, but also to lack of simultaneous development among individuals of a species, and this in turn perhaps reflects inequalities of storage or of access to stored foods.

Of the four hard winters of the decade, 1935-36, 1939-40, 1942-43, and 1944-45, only the first shows consistent lateness in Items 1 to 4. This was also the hardest of the four for wintering animals (Erington, 1945).

Winter snow cover may greatly advance the spring development of plants which winter as "rosettes," or which otherwise retain green leaves. Thus in 1945, after nearly continuous snow cover, chickweed bloomed on March 20, whereas uncovered chickweed, being frozen, usually shows no bloom until May.

Late spring frosts may either destroy the bloom of plants, injure the buds so that no bloom develops, or injure the plant so that bloom is deferred. Thus all oak catkins on flat lands were killed by the frost of April 27-28, 1946.

The same frost injured lilac buds at the Sauk station so that further development ceased, and the buds eventually died. An erroneous observation of "not yet in bloom" might be made on such inhibited buds.

The same frost injured a lupine plant at the Sauk station. While other lupines bloomed normally from May 5 to June 23, this plant was yellow, undersized, and barren. On July 19, a week after uninjured lupines had shed their last seeds, the injured plant burst into vigorous bloom. Had it not been under special observation, a completely abnormal blooming date might have been recorded as normal phenology.

Some frost injuries to trees are "stratified." Thus in 1945 and 1946 frosts killed the lower blooms and leaves of some black and white oaks, leaving the tops of the same trees undamaged and able to bear mast.

In years of late spring frosts it is only the intra-specific variability of blooming dates in oaks which saves any mast at all. This variability in oaks must have been of great importance to the passenger pigeon, which depended on mast of the previous year for food during nesting.

DROUTH, TEMPERATURE, AND FLOOD EFFECTS

Once in a while a phenological record is accompanied by weather changes which seem to isolate some factor in plant or animal development. When this happens there is a chance to deduce the response of a whole community to its weather environment.

The most important opportunity which arose during this study has already been described in the discussion of phenographs. Some additional "natural experiments" on plants will now be considered briefly. Laboratory experiments on single species

under controlled conditions cover the same ground, but much more accurately. The only claim for these cases is that whole plant communities cannot be manipulated under laboratory conditions.

All deductions from "natural experiments" are beset with the difficulty of distinguishing immediate responses from lag effects. The weather often does not permit the identification of lag effects.

DROUTH AND FIRST BLOOM

The most intense drouth of the decade extended from April 10 to August 10, 1936. Our dates for this year are too meagre to yield any measurement of how this drouth affected phenology.

Four milder drouths covered the month of July in 1937, 1939, 1940, and 1941. The date of first bloom in 20 forbs and grasses during these four Julys shows no conclusive retardation or acceleration except in 1941, when July blooms were early. This was probably momentum-earliness from a warm April, May, and June in 1941.

July, 1946, while outside the period covered by this report, offers a chance to check on the conclusion that drouth as such does not change the date of current first bloom. The weather was very dry (-2.65 ins.) but the temperature was normal ($+0.8^{\circ}\text{F.}$). At the Sauk station (used because its sandy soils ought to exaggerate drouth effects), 32 forbs starting bloom during July were half early and half late as compared to their own averages. The

average deviation was 1.2 days early. This diversity among species again suggests a lag effect from a very warm May and June, the species having lost their momentum-earliness at different rates, as they did in 1945.

In short, five July drouths show no aberrations in date of first bloom which are not more plausibly ascribed to antecedent temperatures.

DROUTH AND LENGTH OF BLOOM

While no effect of drouth on date of first bloom can be demonstrated, it is possible that drouth might affect duration of bloom. The best comparison is July 1945, which was cool and wet, with July 1946, which was normal in temperature but very dry (-2.65 ins.). Of 19 July forbs terminating before the drouth was broken on September 5, 14 terminated earlier and five later than in the cool wet 1945. The average deviation was seven days shorter bloom in 1946. Since the average temperature in 1946 was normal, it seems likely that the preponderance of shortened bloom was due to drouth. The diversity among species is worthy of note. No marsh species were used.

TEMPERATURE AND LENGTH OF BLOOM

The hot wet June of 1944 is now compared for duration of bloom with the cool somewhat dry June of 1945. Both stations are used. The comparison is so striking that the detail for one group of eight woods forbs is given as follows:

	1944	1945	Difference
June temperature, departure from mean.....	$+2.4^{\circ}\text{F.}$	-4.6°F.	7°F. colder, 1945
Precipitation, departure from mean.....	$+2.62$ ins	-0.49 ins.	3.1 ins. dryer, 1945
78 Small-flowered crowfoot.....	18 days	62 days	
104 White trillium.....	16, 18	36, 42	
118 Jack in the pulpit.....	11	20	
128 Waterleaf.....	27	35	
129 Columbine.....	22	41, 44	
135 Wild geranium.....	25	30, 46	
139 Tall yellow ladyslipper.....	15	30	
149 Golden ragwort.....	15, 20	17, 41	
Average.....	19 days	35 days	84 percent longer, 1945

Eight prairie forbs, analyzed in the same manner, bloomed an average of 27 days in 1944 and 43 days in 1945, again 60 percent longer during the cooler June.

Ten woody plants bloomed an average of 14 days in 1944 and 24 days in 1945, again 71 percent longer during the cooler June.

In short, the cool June of 1945 prolonged the duration of bloom 60 to 84 percent in three groups aggregating 26 species. This prolongation is so pronounced as to leave little room for doubt. Despite abundant moisture, blooming periods were short during the hot June of 1944, but long during the cool June of 1945. It appears that heat was the prime cause of short duration in June, 1944.

FLOOD EFFECTS

On June 3, 1943, the Wisconsin River at the Sauk station overflowed the sandy old fields which are the habitat of *Penstemon gracilis* [162]. This species had developed flower buds by May 31, and the buds were about to open when flooded. The flowers were all killed, though the plants survived and bloomed normally in 1944.

Floods may have opposite effects on the bloom of different species growing at slightly different levels. Thus ragweed [298] on the sandbars of the Wisconsin River may not bloom at all in dry years unless sub-irrigated by a rise of the river in mid-summer, whereas the same rise of water may flood and destroy such flowers as *Mimulus ringens* and

Bidens [307] which have sprung up on the receding shoreline of the same sandbar.

The two preceding paragraphs deal with the destruction of blooms by floods. An even more common case is the distortion of blooming phenology in annuals germinating on a receding shoreline. *Polygonum* and *Bidens* often show a zonal phenology on such sites, the earliest plants occurring on the higher levels, with cumulative distortion progressing toward the lower levels. All phenology from such sites is unrepresentative.

COMPARISON BETWEEN STATIONS

The dates of developmental phenomena are influenced by latitude, longitude, and altitude. The direction and magnitude of these factors is expressed, in mass data, by Hopkins' (1918) law, which asserts that: "Other conditions being equal, the variation in the time of occurrence of a given periodical event in life activity in temperate North America is at the general average rate of four days to each degree of latitude, five degrees of longitude, and 400 feet altitude, later northward, eastward, and upward in the spring and early summer."

Tables 1 to 12 offer a suitable variety of events for a mass comparison with Hopkins' Law, but the distance between the two stations is too small to be advantageous for this purpose. Nevertheless, as Hopkins points out, his formula may be used not only to predict the average difference between localities, but to evaluate the intensity of the local factors which cause local deviations from the law. From this viewpoint a comparison of our two stations is worth making.

ELIGIBLE DATES

All of the animal data are excluded, because of the difficulty, already explained, of interpolating animal dates between weekly visits to the Sauk station.

All pairs of plant dates in which a given plant

event was recorded at both stations during the same year are included. There are 241 such pairs from April to June, inclusive, and 96 in July and August, a total of 337. Because Hopkins specifies "spring and early summer" it seems advisable to segregate the midsummer data. All items lacking sharpness, such as budding, ripening of fruit, and harvesting of crops are excluded. What remains is entirely dates of first bloom.

SAUK VS. DANE STATIONS

Table 15 presents a summary of the eligible data by months. For the period April to June, the Dane station averages 3.3 days earlier than the Sauk station, and each of the component months shows a two or three day difference. In July, however, the difference is four days, and in August (on meagre data) seven days.

TABLE 15. Difference in 337 Pairs of Dates of First Bloom, Sauk and Dane Stations, 1935-45.

Month	Dane Earlier in		Sauk Earlier in		Total		Average Days Earlier at Dane
	Pairs	Total Days	Pairs	Total Days	Pairs	Net Total Days	
April.....	36	163	10	45	46	118	2.6
May.....	81	519	19	153	100	366	3.6
June.....	70	442	25	142	95	300	3.2
April-June..	(187)	...	(54)	...	(241)	(784)	(3.3)
July.....	66	434	15	68	81	366	4.5
August.....	14	117	1	4	15	113	7.5
April-August	267	...	70	...	337	1263	3.7

Hopkins' Law

The observed three-day difference for the April-June period is now to be compared with the expectation-difference under Hopkins' Law.

Latitude: Sauk Station 43° 36' North	
Dane Station 43° 5' North	
Difference 31' ÷ 60' = 0.52° x 4 days =	2.08 days later
Longitude: Sauk Station 89° 40' West	at Sauk
Dane Station 89° 25' West	4
Difference 15' ÷ 60' = 0.25° x — days =	0.20 days earlier
	5
Net.....	1.88 days later
	at Sauk
Altitude: Dane (Lake Mendota) 849 feet above sea level	
Sauk (Wis. R. at Dells) 815 feet above sea level	
Difference 34 feet ÷ 400 feet = .085 x 4 days	= 0.34 days
	earlier at
	Sauk
Net expectation	1.54 days later
	at Sauk

The Sauk station, in short, averages about three days later than Dane according to our observed blooming dates, whereas Hopkins' Law would lead one to expect only about a day and a half. This distortion of Hopkins' Law either reflects some undetected error, or it measures the net strength of unknown local factors which tend to make the Dane station earlier or the Sauk station later than their geographic positions alone would indicate.

Since both stations lie on the common frontier of three biotic provinces, local factors might well be more influential than within the interior of any one province.

Of the various possible errors, the one most likely to affect Table 15 would be the "Town vs. Country" error, for there is no urban area at Sauk. However, the urban error is believed to be inoperative by June, whereas the earliness of the Dane station persists beyond June. Also the earliness of the Dane station is least in April (2.6 days). It should be greatest in April if distorted by this error. It seems unlikely, therefore, that this particular error accounts for the difference between stations.

Hopkins seems to have derived his formula from a few plants and insects in many localities. We derive our values from many plants in two localities. Our data seem to indicate that species respond differently to the combination of local weather and astronomic constants like length of day. If this is true, one might expect some non-conformity with Hopkins' Law.

In the case of the Sauk station, the tendency toward late spring frosts, working in combination with the prolongation or momentum effects demonstrated in this paper, might well have the effect of distorting Sauk phenology in the direction of lateness

through the spring and early summer. On the other hand the writers have often received the impression that the warm sands at Sauk, on certain sites and in certain early-spring sand species, distorted the Sauk record in the direction of earliness. These contradictory distortions probably exist, but their "valences" vary in such complex patterns that the mind cannot follow them.

There is danger of over-simplifying one's mental picture of a phenological formula like Hopkins' Law. Table 15 shows that the Sauk station was by no means always late; it was early in 70 cases (pairs of dates) and late in 267. Moreover a single species often showed alternation between the two stations in successive years. All this again indicates that phenology reflects the interplay of many variable factors, rather than the continuous domination of any single factor.

COMPARISON OF 1880's AND 1940's

Three published phenology records were found for localities in or near the stations covered in this study. These will now be compared with our records.

HENRY'S PHENOLOGY, 1881-1885

This record was started by Dean W. H. Henry (1881) of the Wisconsin College of Agriculture, and was carried through under his supervision by a succession of his graduate students (Trelease, 1884 & 1885).

In Table 16, 18 items common to Dean Henry's record are compared with those for the Dane station. It should be noted that his record ends with May, but that the items are well spread in time, and are carried through the four-year period with considerable persistence.

TABLE 16. Phenology for Madison (Dane Station) 1880's vs. 1940's. Data for 1881 from Henry (1881), for 1883-1885 from Trelease (1884, 1885).

Species	Item No.	Recent Aver.	1881	1883	1884	1885	Aver. 1881-1885	Deviations				Average Lateness 1881-85
								1881	1883	1884	1885	
MARCH												
Silver maple, pollen	26	3/31	4/17	+17
APRIL												
Lake Mendota, open	27	4/1	5/1	4/13	4/15	4/20	4/20	+20	+12	+14	+19	+19
Hazel, pollen	38	4/2	4/17	4/23	4/20	+15	+21	+18
American elm, pollen	46	4/9	4/15	4/26	4/21	+6	+17	+12
Aspen, pollen	41	4/10	4/20	+10
Cottonwood, pollen	45	4/13	4/19	4/28	5/3	4/27	+6	+15	+20	+14
Box elder, pollen	47	4/14	4/17	4/28	5/10	4/28	+3	+14	+26	+14
Wild plum, bloom	92	4/29	5/13	5/10	5/11	+14	+11	+12
MAY												
Black oak, pollen	88	(5/3)	5/29	+26
Lilac, bloom	113	5/3	5/20	5/25	5/22	+17	+22	+19
White oak, pollen	88	(5/5)	5/18?	5/23	5/21	5/21	+13	(+18)	(+16)	(+16)
Sugar maple, pollen	97	5/5	5/17?	5/19	5/18	+12?	+14	+13
Chokecherry, bloom	100	5/8	5/16	5/20	5/27	5/21	+8	+12	+19	+13
American elm, fruit	46	5/12 (Sauk)	5/26	6/3	5/20	+14	+22	+18
Asiatic honeysuckle, bloom	123	5/13	6/1	+19
Silver maple, fruit	26	(5/15)	5/31	(+16)
Black raspberry, bloom	150	(5/23)	5/27	6/13	6/4	(+4)	(+21)	(+12)
Black locust, bloom	175	5/29	5/27	6/15	6/6	-2	+18	+8
Average lateness, 1881-1885, in days								+15	+13	+14	+19	+15

Of the 37 deviations from the average dates shown in Table 16, only one (black locust, 1881) bears a minus sign. That is to say, the early 1880's were uniformly later in their spring phenology than the 1940's, and the magnitude of the deviation is pre-vaillingly large, averaging over two weeks (see bottom line of table).

Such a uniform deviation raises the question: was the weather also uniformly cold? The deviation from monthly mean temperature, according to the U. S. Weather Bureau were:

	Mean of 107 years	1881	1883	1884	1885
February....	20°F.	-1°F.	-3°F.	-4°F.	-16°F.
March.....	31°F.	-2°F.	-4°F.	-4°F.	-6°F.
April.....	45°F.	-5°F.	+1°F.	-2°F.	-3°F.
May.....	57°F.	+4°F.	-4°F.	-1°F.	-2°F.

In short, only two months out of the 16 were above normal in temperature; all the rest were cold, and some very cold. There were two warm months, May 1881 and April 1883. The former shows the only minus sign in Table 16; black locust was two days early. April 1883 was only one degree above normal. Its phenology was uniformly late, no doubt due to the "momentum" of the preceding March cold.

The warm May of the cold spring of 1881 was especially noted by Dean Henry, who says: "The large masses of snow . . . neutralized the rays of the sun and long delayed the coming of spring, but when vegetation once started into life, it was with that celerity which is so characteristic of alpine and polar regions."

The coldness and lateness which prevailed during the early 1880's raises the question: was this period the low phase in a climatic cycle? The best answer is found in Wing's (1943) graph of the opening and closing dates for Lake Mendota. During the entire period 1879-1886 Mendota opened late and closed early. During the decade 1935-1945 Mendota opened early in nine out of 11, and closed late in ten out of 11 years. It is clear that Dean Henry's record coincides with a cold period, and that in this paper with a warm period.

Whether these fluctuations are segments of a recurring cycle is another question which only time can answer.

HOUGH'S PHENOLOGY, 1851-1859

During this decade, the volunteer weather observers of the Smithsonian Institution were asked, by circular letter, to record a standardized phenology on 229 items covering "the date of putting forth and fall of leaves, blossoming, ripening of fruit, [and] times of appearance and disappearance of animals." The data were compiled by Franklin B. Hough and published in 1864.

Of some 300 stations at which observations were recorded, three lie within or near the areas covered in this study. These were Madison (Dane station), Baraboo (Sauk station), and Milwaukee (50 miles

east of Dane, but on Lake Michigan, and hence not properly comparable). These stations recorded 26 items common to our record, but few of these cover more than a single year, 1851. These 26 items have been analyzed by the same method used in Table 16. The analysis shows no large or consistent difference between 1851 and the recent average. The data do not seem worth including in this paper, especially since there is no assurance that the recorders were equally competent or adhered to any uniform standard.

SUMMARY

A decade of dates of 328 seasonal events at two stations, 33 miles apart, were analyzed and compared with prior records.

Spring events during the decade 1935-1945 were two weeks earlier than the same events at the same station in 1881-1885.

The northern station is three days later in spring than the southern one, which is twice the expectation under Hopkins' Law. The difference between the two stations is least in early spring and greatest in midsummer.

The year-to-year variability of events, as compared with their own averages, tends to be greatest in early spring, and decreases progressively through May.

Some plants show little variability in date of first bloom; they seem to be governed more by length of daylight than by current weather. White clover, the least variable plant, has a standard deviation of 2.4 days, which is only a third of that prevailing in other plants during the same month.

Some birds show little variability in arrival date, despite the fact that they winter in or beyond the tropics where changes in length of day are much less pronounced. The least variable birds were rose-breasted grosbeak (3.1 days) and upland plover (3.2 days), both only a third of the deviation prevailing in other contemporary migrants.

Bird migration responds to changes in temperature much more quickly than the bloom of plants. In 1945 the momentum of an early warm period persisted in plants through two months of subsequent cold. This momentum caused early bloom in white trillium despite the fact that it was still underground during the warm period.

Duration of bloom in a cool dry June, as compared with a hot wet June, was protracted 60 to 84 percent in various groups of plants.

Dates of first bloom in five dry Julys did not differ from average except in two years, which were early, probably by reason of antecedent heat. In one very dry July, drouth seemed to shorten duration of bloom.

Phenological records are subject to many errors, but these do not affect all species or seasons alike. A comparison of two independent phenologists show a third of 39 pairs of dates identical, a third up to two days apart, and a third up to 11 days apart.

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